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

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Missouri Department of Conservation

Final Report

June 12, 2012

Abstract

Small impoundments provide close-to-home fishing opportunities for anglers but may not support desirable sport fisheries. Most of these fisheries are managed by harvest regulations but watershed 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 largemouth bass *Micropterus salmoides*, bluegill *Lepomis macrochirus*, redear sunfish *L. microlophus*, white crappie *Pomoxis annularis*, and black crappie *P. nigromaculatus* among small Missouri impoundments. Using regression analysis, we found variables associated with predation, competition, and lake fertility were most important in explaining variation in sport fish demographics. 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. Few largemouth bass in these lakes reached large sizes owing to density-dependent growth. Density dependent growth was common among all sport fish species. White crappies, black crappies, and redear sunfish had better growth and size structure in lakes with fewer bluegills, suggesting competition among these species. Lakes containing common carp had fewer largemouth bass and slower-growing black crappies than lakes without common carp. Gizzard shad benefitted largemouth bass populations but harmed bluegill and black crappie populations. Growth and size structure of sport fishes usually improved with increasing lake fertility. Harmful effects of high nutrient concentrations on sport fish populations, however, may occur in hypereutrophic lakes. Our findings support the importance of manipulating largemouth bass densities via harvest restrictions to improve either largemouth bass or panfish populations. It also documents the importance of maintaining adequate nutrient levels to sustain these fisheries.

Small impoundments 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 sport fishing. 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.

While numerous, many of these small public impoundments do not support desirable sport fisheries. Commonly, growth, size structure, or both are poor for one or more sport fish species. There are probably many causes for these undesirable populations including overharvest, poor water quality and habitat, and deleterious species interactions. Early studies of these systems documented overharvest of largemouth bass *Micropterus salmoides*, which led to restricting angler harvest by imposing minimum length limits (Funk 1974) and later 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 many anglers practice voluntary catch-and-release (Quinn 1996; Siepker et al. 2007; Myers et al. 2008). High angler exploitation of other common species such as bluegill *Lepomis macrochirus*, black crappies *Pomoxis nigromaculatus* and white crappies *P. annularis* (Coble 1988; Eder 1990; Bister 2002), can result in poor fish size structure by the direct removal of large fish and shifts in life history strategies (Beard et al. 1997; Drake et al. 1997). Although, length limits have also been imposed in some small impoundments, these regulations frequently did not improve fish size structure and were not 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).

Water quality and habitat within small impoundments, as determined by watershed characteristics including 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 nutrients than those in forests (Jones et al. 2004). Within either landscape type, impoundments with large flushing rates, 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 fertility (Hanson and Leggett 1982; Jones and Hoyer 1982). Growth and size structure of sport fishes are commonly 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 greater prey abundance in more fertile waters. In highly fertile systems, however, undesirable fish species are common (Bachmann et al. 1996; Egertson and Downing 2004). McInerny and Cross (1999) found that first-year growth of black crappies increased with chlorophyll concentrations up to a threshold of ≈ 100 μg/L, after which growth was reduced. This finding suggests excessive nutrients may lead to undesirable growth and size structure of sport fishes similar to the relationship observed for biomass. Many of these systems also suffer from low dissolved oxygen and periodic fish kills (Moyle 1949; Mericas and Malone 1984)

Abundance, growth, and size structure of sport fishes have been also been linked to 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 McInery 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 demographics, 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 in Minnesota lakes (Tomcko and Pierce 2001). Similarly, the relationships between aquatic macrophyte coverage and sport fish demographics have been mixed. Dibble et al. (1996) suggested that 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 depletion of food resources. Others have not detected this unimodal relationship between sport fish growth and plants (Savino et al. 1992; Cheruvelil et al. 2005). Instead several studies have reported a negative relationship between plant density or coverage and largemouth bass growth (Hoyer and Canfield 1996; Pothoven et al. 1999; Paukert and Willis 2004; Cheruvelil et al.

2005). Bluegill growth can be inversely related (Cheruvelil et al. 2005) or unrelated (Savino et al. 1992) to plant coverage or density. Yet, some lakes with extensive macrophyte coverage contained fast-growing bluegills (Schneider 1999). Growth of crappies may not be related to macrophyte coverage (Allen et al. 1998) except that growth may be depressed in densely vegetated waters (Maceina and Shireman 1985). Sport fish abundance is thought to increase with macrophyte coverage, especially in the littoral zone (Dibble et al. 1996); but some studies have found no relationship (Hoyer and Canfield 1996; Allen et al. 1998).

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 common carp *Cyprinus carpio* and gizzard shad *Dorosoma cepedianum* can result in undesirable 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 influences affect sport fish populations in small impoundments with uncertainty about which variables are most important. 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 among watershed, impoundment, water quality, and species interaction variables is necessary.

In this study we examine the relative importance of these variables among 156 small Missouri impoundments using regression analysis. 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, bluegill, redear sunfish *L. microlophus*, white crappie, and black crappie among small impoundments at a statewide scale. This information will be useful in describing patterns and determining management strategies for improving sport fish populations.

METHODS

Study sites.—Variables influencing sport fish demographics were examined among 156 small impoundments (hereafter termed "lakes") scattered across the state of Missouri. Most lakes were located in the Glacial Plains physiographic section of the state (N = 83), with fewer lakes in the Ozark Border (N = 25), Osage Plains (N = 22), Ozark Highlands (N = 22), Mississippi Lowlands (N = 3), and Big Rivers (N = 1) physiographic sections (see locations of physiographic sections in Figure 1 of Jones et al. 2008b). Small lakes were included in this study if both sport fish and water quality data were available. These lakes spanned the broad range of conditions representative of Missouri's small lakes. Study lakes ranged in size from 2 to 432 ha and in trophic state from oligotrophic to hypereutrophic (Table 1). Watersheds were also diverse including those that were mostly forested to those consisting primarily of cropland or mostly urbanized. Fish populations consisted primarily of largemouth bass, bluegill, 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-mm to 384-mm slot TL 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 to 30 fish for sunfish and crappies and four fish for catfish (*Ictalurus* and *Pylodictis* spp. combined).

Fish data.—Sport fish demographic data were obtained from standardized spring electrofishing surveys conducted during 1969 to 2009 by Missouri Department of Conservation (MDC) fisheries management biologists. However, most data were collected from the late 1970s and later. Surveys were conducted nearly annually in some lakes but only occasionally in others (mean = 11.9 sample years, range = 1 to 34 years). For a sample year, one or more electrofishing surveys were conducted during late April to early June. Electrofishing effort averaged 1.6 hours (range, 0.22-11.27 hours) per sample year in each lake. Fish 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 five per 12.7 mm TL group). Fish with assigned ages were used to construct an age-length key which was then applied to the entire sample to estimate mean length at age. Sampling was conducted mostly during the day in turbid lakes and during the night in clear lakes; however, some lakes were sampled during the day or night depending on the year. Diurnal timing of sampling could affect our estimates of sport fish demographics. Electrofishing catch rates of bluegill 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 bluegill 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 affect our estimates of catch rates but consider this potential bias relatively minor given the large range in catch rates among the study lakes (Table 2).

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 for fish stock size and larger (CPE, number of fish/hour of electrofishing), proportional size distribution (Guy et al. 2007) for quality size (PSD) and preferred size fish (PSD-P), and mean TL at age 3 (mm, ML3) were determined for largemouth bass, bluegill, redear sunfish, white crappie, and black crappie. Total lengths of stock, quality, and preferred size for these species are reported in Anderson and Gutreuter (1983). Mean length at age 3 was chosen for our growth variable because it was the standard parameter reported in lake management reports. Not all fish variables were available for every lake; datasets for largemouth bass and bluegill were the most complete because these fish were the primary targets for the 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. We consider these averages to be the best representation of sport fish demographics for these lakes.

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

Environmental data.—Watershed, lake morphometry, and water quality data (Table 1) were largely from Jones et al. (2004, 2008a, 2008b). Percentages of land-use types within watersheds were determined from 1993 land-use coverage data created by the Missouri Resources Assessment Program (Jones et al. 2004). Dam height was used as a surrogate for water depth (Jones et al. 2004). Limnological data were sampled seasonally on three or four occasions during May-August from surface waters near the dam of each lake. Detailed sampling and analytical procedures are described in Jones et al. (2008a, 2008b). Some additional unpublished water quality data were obtained using these same methods. Limnological data were collected between 1978 and 2009. Shoreline development index (SDI) was calculated as the ratio of the lake perimeter (determined with geographic information system software) to the circumference of a circle with the same area as the lake. Aquatic macrophyte coverage (VEG) was indexed as absent, moderate or abundant by MDC fisheries management biologists. However, for analysis (see below) we lumped absent and moderate VEG into one category. Therefore, VEG was indexed as sparse (index = 0) or abundant (index = 1).

As with fish data, frequency of annual collections of limnological data varied among lakes with some lakes being sampled nearly every year while others were sampled only once (mean = 4.9 sample years, range = 1 to 21 years). We attempted to match limnological data with fish data collected during the same time period. However, in some cases (< 20%) when that was not possible we used long-term average limnological data presented in Jones et al. (2008b) or available data. As for fish data, we averaged limnological data over all sample years for lakes with more than one year of data. Limnological data were, however, averaged for separate time periods for the five lakes where either common carp or gizzard shad presence or absence varied among years.

Analysis.—Prior to using regression analysis, we reduced the number of environmental variables using principal component analysis (procedure PRINCOMP, SAS 9.2, SAS Institute). All variables (Table 1) were included in this analysis. The correlation matrix was used as input for the analysis. Summer water temperature and dissolved oxygen data were not available for as many lakes as the other environmental variables and a preliminary analysis indicated that these variables were not strongly correlated with the principal components that explained the majority of the variation. Consequently, these two variables were dropped from the final analysis. Following procedures of Cross and McInerny (2005), we used environmental variables that were highly correlated to individual principal components as proxy variables instead of principal component scores in the regression analysis. Using actual environmental variables allowed for easier interpretation of relationships between environmental and fish variables.

We used regression analysis (procedure REG, SAS 9.2, SAS Institute) to assess relationships between environmental 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) and enabled us to compare competing models with an information-theoretic approach (Burnham and Anderson 2002). Explanatory variables chosen to be included in regression models included environmental variables determined from the principal component analysis, various sport fish demographic variables (Table 3), and dummy variables for VEG, common carp, and gizzard shad. Prior to analysis, we transformed fish and environmental variables (except dummy variables) using either $\log_e(X)$ or arcsine ($X^{0.5}$) (for proportional data) to normalize the data. Mean length at age 3 data were normally distributed and were not transformed. We included those sport fish demographics that could be associated with competition or predation 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 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). Possibly, redear sunfish and crappies affect largemouth bass and bluegill populations and each other; however, we did not include demographic variables as explanatory variables because data were not available for many lakes.

We compared the fit of various combinations of explanatory variables using the information-theoretic approach (Burnham and Anderson 2002) and considered all models with a difference of Akaike's information criterion (AIC) values of two or less from the most parsimonious model to be statistically similar. To avoid over fitting the models, we restricted the maximum number of explanatory variables to four for all dependent variables except for mean length at age 3 for redear sunfish (maximum number = 3), white crappie (maximum number = 3), and black crappie (maximum number = 2) due to small sample sizes. Preliminary analysis indicated models with additional variables did not significantly improve model fits. Models were only included for consideration if they did not exhibit multicollinearity among the regressors. Models were checked for multicollinearity using diagnostic tools in PROC REG (options VIF, TOL, and COLLINOINT). We sought the simplest models with an AIC ≤ 2 for each dependent variable. Models with the same explanatory variables as a model with a smaller AIC value but with more variables were not presented.

RESULTS

The study lakes exhibited a diverse array of environmental and sport fish characteristics. Lakes varied from shallow to deep, oligotrophic to hypereutrophic, having simple to complex shorelines, and being void of aquatic macrophytes to being extensively vegetated (Table 1). Land use within the watershed also varied from mostly cropland or urbanized to almost entirely forest. Likewise, sport fish demographics varied from low to high relative abundance, small to large size fish, and slow to fast growth (Table 2). Common carp were present in 62 lakes, absent from 53 lakes, and in three other lakes their presence varied over time. Common carp data were missing for 38 lakes. Gizzard shad were present in 77 lakes, absent from 41 lakes, and in five other lakes their presence varied over time. Gizzard shad data were missing for 33 lakes.

The number of potential explanatory environmental variables was reduced to eight using principal components analysis. The first six principal components (PC1 - PC6) explained 77% of variance in the dataset. The seventh and following principal components each explained less than 5% of additional variance and were excluded from further consideration. Total phosphorus, total nitrogen, and Secchi depth were most strongly correlated with PC1 (Table 4). We chose total phosphorus (TP) as a proxy variable for PC1 because it is strongly correlated with all trophic state metrics in Missouri reservoirs (Jones et al. 2008b) and data were available for all lakes. Lake surface area (SA) and SDI were most strongly correlated with PC2 and were both used as proxy variables for this component. These variables describe the size and shape of the lake. The watershed/lake surface area ratio and the flushing index were most strongly correlated with PC3 and the watershed/lake surface area ratio (WSA) was used as the proxy variable. Urban land cover (URBAN) and chlorophyll concentration (CHL) were used as proxy variables for PC4 and PC5, respectively. For PC6, non-volatile solid concentration (NVSS) was available for every lake and used as the proxy variable even though grass land cover had a higher correlation coefficient. Thus, in addition to VEG, TP, SA, SDI, WSA, URBAN, CHL, and NVSS were included as potential environmental variables in the regression models.

Largemouth Bass Models

Variations in largemouth bass demographics were primarily explained by lake fertility and fish variables (Table 5). Relative abundance of largemouth bass was positively associated with bluegill CPE and negatively associated with TP, common carp presence (Figure 1A), and WSA. Largemouth bass PSD increased with increasing lake fertility (TP and CHL), the abundance of small bluegills (low PSD and high CPE), and gizzard shad presence, and decreased with increasing largemouth bass CPE (Figure 1B and C). The morphometric variables SA and SDI, NVSS, and common carp presence also were included in some PSD models but were of lesser importance. Models for largemouth bass PSD-P had similar relationships to PSD (Figure 1D). Mean length at age 3 for largemouth bass increased with increasing SA and bluegill CPE and decreased with increasing NVSS (Figure 1E and F). Gizzard shad presence had a slightly negative effect on ML3 (Figure 1F). Largemouth bass ML3 was also positively associated TP, CHL, and SDI, and negatively associated with URBAN, although the latter two variables explained less than two percent of the variation in ML3.

Bluegill Models

Bluegill demographics were most strongly associated with fish variables and to a lesser degree, lake fertility (Table 6). Relative abundance of bluegills was positively associated with the largemouth bass CPE and PSD-P (Figure 2A), TP, and CHL, and negatively associated with gizzard shad presence and NVSS. Bluegill PSD was positively associated with the abundance of small largemouth bass (i.e., high CPE and low PSD-P) and CHL, and negatively associated with

NVSS (Figure 2B and C) and bluegill CPE. Bluegill PSD-P was greatest in lakes with large numbers of largemouth bass, no gizzard shad, low NVSS, and small numbers of bluegills (Figure 2D and E). Bluegill ML3 was negatively associated with largemouth bass PSD-P and gizzard shad presence, and positively associated with CHL (Figure 2F).

Redear Sunfish Models

Redear sunfish demographics were mostly associated with fish and lake fertility variables (Table 7). Relative abundance of redear sunfish was negatively associated with largemouth bass PSD and PSD-P and CHL, and positively associated bluegill CPE and VEG (Figure 3A and B). Other explanatory variables were of lesser importance and were all negatively associated with redear sunfish CPE. Redear sunfish PSD increased with decreasing redear sunfish CPE and increasing lake fertility (Figure 3C). Other explanatory variables explained less than three percent of the variation in redear sunfish PSD. Redear sunfish PSD-P was negatively associated with redear sunfish CPE and positively associated with largemouth bass CPE (Figure 3D). Of lesser importance were positive associations with CHL and TP, and negative associations with bluegill CPE and largemouth bass PSD-P. Redear sunfish ML3 was most strongly and positively associated lake fertility variables and SA (Figure 3E), with several other variables of lesser importance.

White Crappie Models

White crappie demographics were primarily associated with fish variables, NVSS, and SA (Table 8). White crappie CPE was positively associated with NVSS, gizzard shad presence, bluegill CPE, largemouth bass PSD-P, and SA. The most important variables were either a combination of NVSS, bluegill CPE, and gizzard shad presence/absence (Figure 4A) or NVSS and SA (Figure 4B). White crappie PSD increased with decreasing bluegill CPE and white crappie CPE (Figure 4C) and increasing largemouth bass CPE. The most important explanatory variables for white crappie PSD-P included largemouth bass CPE and PSD, bluegill CPE, white crappie CPE, and SA. White crappie PSD-P was highest in larger lakes with high largemouth bass CPE and low bluegill CPE (Figure 4D and E) and low white crappie CPE. White crappie ML3 was negatively associated with white crappie CPE and largemouth bass PSD and PSD-P, and positively associated with CHL and SDI. Lakes with low white crappie CPE and low largemouth bass PSD-P or PSD contained the largest white crappie at age 3 (Figure 4F).

Black Crappie Models

Black crappie demographics were mostly associated with fish variables and to a lesser extent lake fertility and morphometric variables (Table 9). Black crappie CPE was weakly, but positively associated with largemouth bass PSD and CPE (Figure 5A). Black crappie PSD was positively associated with largemouth bass CPE and VEG, and negatively associated with black crappie CPE (Figure 5B) and WSA. Black crappie PSD-P was negatively associated with the presence of gizzard shad, black crappie CPE, largemouth bass PSD and PSD-P, and WSA, and positively associated with CHL, largemouth bass CPE, and SA. The best models included a combination of black crappie CPE, WSA, and gizzard shad presence/absence (Figure 5C) or CHL and black crappie CPE (Figure 5D). Sample sizes for black crappie ML3 models were small but these models revealed that ML3 was largest in lakes with few bluegills, abundant small largemouth bass (high CPE and low PSD and PSD-P), and without common carp (Figure 5E and F). Black crappie ML3 was also negatively associated SDI, SA, and black crappie CPE, and positively associated with WSA.

DISCUSSION

Variables associated with predation, competition, and lake fertility were most important in explaining variation in sport fish demographics. There was evidence for competition both within and among species and density-dependent growth was observed for every sport fish species. As 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). Few lakes contained large numbers of both large largemouth bass and large sunfish and crappies. As previously reported, size structure and growth within a given species were poorer with increasing density (Guy and Willis 1995; Pope et al. 2004; Tomcko and Pierce 2005). Interspecific competition may also structure sport fish populations in these small lakes.

Size structure of white crappies and redear sunfish and growth of black crappies declined with increasing bluegill abundance, suggesting food competition. Cichra et al. (1983) found lakes dominated by intermediate-size bluegills (100-159 mm TL) contained stunted white crappie populations, congruent with our findings. Gabelhouse (1984) found a positive relationship between crappie PSD and bluegill PSD, possibly because bluegill abundance was lower in lakes with higher bluegill PSD. Interestingly, bluegill CPE was positively correlated with largemouth bass CPE, redear sunfish CPE, and white crappie CPE. While 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 conditions suitable for recruitment are similar among these species.

Common carp and gizzard shad exhibited variable effects on sport fish populations. Lakes with common carp had lower abundances of largemouth bass and slower growth of black crappies; however, few other negative effects on sport fish species were found. Common carp seem to negatively affect sport fish when they reach an abundance threshold, beyond which abundances of sport fishes are reduced (Jackson et al. 2010; Weber and Brown 2011). Unfortunately, we lacked the data necessary to examine these relationships in our study lakes. Common carp are known to destroy aquatic macrophytes (Parkos et al. 2003; Weber and Brown 2009), which reduces nursery areas for juvenile fishes and potentially sport fish recruitment. Elimination of aquatic macrophytes and benthic foraging by common carp may also reduce macroinvertebrate densities which in turn may reduce growth of fishes that feed on these prey (Parkos et al. 2003; Wahl et al. 2011). Perhaps growth of black crappies, which are known to feed on macroinvertebrates (Ball and Kilambi 1973; Ellison 1984; Tuten et al. 2008), suffered in lakes with common carp because of lower prey resources. Lakes containing gizzard shad usually had poorer growth and size structure of bluegills and smaller PSD-P values for black crappie but better size structure of largemouth bass than lakes without gizzard shad. While the actual mechanisms are unknown, negative effects of gizzard shad on bluegill have been commonly reported (Aday et al. 2003; Michaletz and Bonneau 2005; Porath and Hurley 2005). Conversely, gizzard shad are an important prey for largemouth bass and may improve growth of this predator species (Storck 1986; Michaletz 1997). The negative, albeit weak, relationship between gizzard shad presence and largemouth bass ML3 is puzzling given the positive relationships with largemouth bass size structure variables. The observed negative relationship may be because gizzard shad were frequently present in lakes with high NVSS in which largemouth bass grew more slowly (Figure 1F). Alternatively, due to rapid growth rates of gizzard shad, this prey may not have been available to largemouth bass age 3 and younger and only larger largemouth bass may have benefited from this prey resource (Brummett 1983; Neuswanger 1983). Similarly, gizzard shad may have grown too rapidly to be useful as prey for black crappies (Ellison 1984; Mosher 1984) and may have restricted numbers of quality size black crappies via similar mechanisms that occurred for bluegills.

Increasing lake fertility as measured by either TP or CHL generally enhanced growth and size structure of sport fishes in the study lakes. These variables were positively associated with growth and size structure of largemouth bass, bluegill, redear sunfish, white crappies, and black crappies. However, for black crappie PSD-P (Figure 5D) and largemouth bass PSD (not shown) there seemed to be a threshold at CHL of 40-60 μg/L beyond which these size structure variables declined. Additionally, largemouth bass and redear sunfish CPE declined with increased lake fertility but were especially low for most lakes with TP > 100 μg/L or CHL > 40-60 μg/L. Thus, the relationships between sport fish demographics and lake fertility variables are likely nonlinear (Kautz 1980; McInerny and Cross 1999; Egertson and Downing 2004), but apparently only a few study lakes contained nutrient levels high enough to observe negative effects on sport fish populations.

Other variables were occasionally important in explaining variation in sport fish demographics. Non-volatile suspended solids were 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 more tolerant of turbidity than some centrarchids and can exist in turbid lakes at high densities (Ellison 1984; Muoenke et al. 1992). Typically white crappies in these dense populations are slow growing and most do not reach large sizes (Ellison 1984; Muoenke et al. 1992; this study). Vegetation cover was positively associated with redear sunfish CPE and black crappie PSD. These two species may have benefitted from the gastropods and other 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. Large lakes had more complex shorelines as indicated by the positive correlation between SA and SDI (both $\log_e$-transformed; $r = 0.80$; $P < 0.0001$) and consequently, only one of these two variables were included in a regression model. Largemouth bass grew faster in larger Nebraska lakes (Paukert and Willis 2004) consistent with our findings, whereas, bluegills fared better in smaller Minnesota lakes (Cross and McInerny 2005). We found no significant relationships between bluegills and SA. Finally, two watershed variables, URBAN and WSA, were sometimes included in models with URBAN being negatively associated with sport fish demographics and WSA having both positive and negative coefficients. In most cases, neither variable explained much of the variation in sport fish demographics. Redear sunfish CPE was negatively affected by urbanization in the watershed, but even for this CPE model URBAN explained < 5% of the variance in redear sunfish CPE. The WSA was most important in explaining growth of black crappies. Black crappies grew 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).

Although most models explained less than half of the variation in sport fish demographics, they provide information useful to fisheries managers. Many small lakes are managed exclusively by restricting angler harvest especially of largemouth bass. Our study confirms the importance of manipulating largemouth bass densities to improve largemouth bass or panfish populations. Acceptable sport fisheries for both largemouth bass and panfish can be achieved by maintaining moderate densities and size structure of largemouth bass (Novinger and Legler 1978), provided lake fertility is sufficient. However, it is unlikely that large numbers of both large largemouth bass and large panfish will exist in a lake. To create a panfish population with many large individuals, largemouth bass growth and size structure may have to be sacrificed (Gabelhouse 1984; Willis et al. 2010). High-quality bluegill populations will probably only be achieved in productive lakes with high densities of largemouth bass and no gizzard shad. Conversely, high-quality largemouth bass populations will most likely occur in lakes with low densities of largemouth bass, moderate to high densities of small bluegills, and gizzard shad (Willis et al. 2010). Intense largemouth bass predation and lower abundances of bluegills appear 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 as the importance of watershed characteristics to lake sport fisheries has been recognized (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. These efforts have benefited sport fisheries in lakes that had 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 lifespan of the lakes. Inorganic suspended solid concentrations generally had a negative effect on sport fish populations. However, caution should be used when reducing nutrient input into lakes because 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 only in hypereutrophic lakes is there a potential for harmful effects of high nutrient concentrations on warmwater sport fish populations.

ACKNOWLEDGMENTS

We thank the many current and past biologists and technicians who collected and provided the data used in this study. We also thank Steffanie Abel for her efforts in acquiring and developing the fish dataset. Tim Bixler and Philip Marley provided lake perimeter and surface area data necessary to compute the shoreline development index.

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Table 1. Summary statistics for the environmental variables for the small lakes. For water quality data, five lakes may be represented either two or three 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
Watershed						
Watershed area (ha)	152	1,747	469	495	10	66,622
Forest land cover (%)	153	31.3	2.1	22.5	0	99.3
Grass land cover (%)	153	35.3	1.4	34.9	0.1	76.7
Crop land cover (%)	153	18.4	1.3	14.8	0	74.0
Wetlands (%)	153	0.5	0.1	0.1	0	3.9
Water (%)	153	8.1	0.4	7.7	0	32.6
Urban land cover (%)	153	6.4	0.9	2.9	0	70.5
Lake morphometry						
Lake surface area (ha)	156	51	6	25	2	432
Dam height (m)	151	12.3	0.4	11.6	3.1	33.6
Volume (m^3 x 1,000)	151	2,792	466	860	41	34,146
Watershed area/lake surface area	152	33	6	17	1	592
Flushing index (times/year)	141	3.1	0.9	0.9	0.03	87.0
Shoreline development index[a]	156	2.5	0.1	2.2	1.0	6.3
Water quality						
Chlorophyll (µg/L)	162	23	2	16	1	186
Total phosphorus (µg/L)	162	55	4	43	7	324
Total nitrogen (µg/L)	161	803	28	761	158	2,103
Volatile suspended solids (mg/L)	161	3.9	0.2	3.1	0.3	23.5
Non-volatile suspended solids (mg/L)	162	3.9	0.3	2.9	0.2	37.2
Secchi depth (m)	162	1.2	0.1	1.0	0.2	6.4
Conductivity (µS)	162	197	6	189	40	555
Summer water temperature (°C)	127	26.2	0.1	26.0	23.0	32.0
Summer dissolved oxygen (mg/L)	125	7.8	0.1	7.6	4.7	15.8

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

Table 2. Summary statistics for catch per effort (N/hour of electrofishing) stock size and larger fish (CPE), proportional size distribution for quality size (PSD) and preferred size fish (PSD-P), and mean total length at age 3 (mm, ML3) for largemouth bass, bluegill, redear sunfish, white crappie, and black crappie in the small lakes. Five lakes are represented either two or three 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	161	83	3	80	3	186
PSD	162	43	2	42	0	100
PSD-P	162	17	1	13	0	100
ML3	83	275	4	271	210	364
Bluegill						
CPE	161	140	7	124	15	720
PSD	162	34	1	33	0	85
PSD-P	162	3	0.5	1	0	40
ML3	86	134	2	134	94	184
Redear sunfish						
CPE	72	36	3	26	1	143
PSD	72	66	2	68	16	100
PSD-P	72	25	2	23	0	100
ML3	28	169	5	173	114	211
White crappie						
CPE	94	39	4	23	0	186
PSD	94	48	3	49	0	100
PSD-P	94	16	2	10	0	100
ML3	36	210	6	214	132	290
Black crappie						
CPE	60	17	2	13	1	78
PSD	60	62	3	63	0	100
PSD-P	60	20	3	14	0	93
ML3	15	228	9	235	145	280

Table 3. Sport fish variables used as potential explanatory variables in regression models for the various response variables for largemouth bass (Lmb), bluegill (Blg), redear sunfish (Red), white crappie (Whc), and black crappie (Blc) in the small lakes. See Table 2 for variable descriptions.

	Explanatory variables								
	Lmb			Blg			Red		
Response variable	CPE	PSD	PSD-P	CPE	PSD	PSD-P	CPE	PSD	PSD-P
Lmb									
CPE				x					
PSD	x			x	x				
PSD-P	x			x	x				
ML3	x			x	x				
Blg									
CPE	x	x	x						
PSD	x	x	x	x					
PSD-P	x	x	x	x					
ML3	x	x	x	x					
Red									
SCPE	x	x	x	x					
PSD	x	x	x	x			x		
PSD-P	x	x	x	x			x		
ML3	x	x	x	x			x		
Whc									
CPE	x	x	x	x					
PSD	x	x	x	x					
PSD-P	x	x	x	x					
ML3	x	x	x	x					
Blc									
CPE	x	x	x	x					
PSD	x	x	x	x					
PSD-P	x	x	x	x					
ML3	x	x	x	x					

Table 3 extended. Sport fish variables used as potential explanatory variables in regression models for the various response variables for largemouth bass (Lmb), bluegill (Blg), redear sunfish (Red), white crappie (Whc), and black crappie (Blc) in the small lakes. See Table 2 for variable descriptions.

	Explanatory variables					
	Whc			Blc		
Response Variable	CPE	PSD	PSD-P	CPE	PSD	PSD-P
Lmb						
CPE						
PSD						
PSD-P						
ML3						
Blg						
CPE						
PSD						
PSD-P						
ML3						
Red						
CPE						
PSD						
PSD-P						
ML3						
Whc						
CPE						
PSD	x					
PSD-P	x					
ML3	x					
Blc						
CPE						
PSD				x		
PSD-P				x		
ML3				x		

Table 4. Principal component loadings (correlation coefficients) and the percent of explained variation for the first six components (PC1 – PC6) on environmental variables for the study lakes. Loadings in bold indicate the variables that were selected to be included in regression analyses. See Table 1 for variable units.

Variable	PC1	PC2	PC3	PC4	PC5	PC6
Watershed area	-0.069	0.207	0.421	-0.091	0.054	0.123
Forest land cover	-0.283	-0.243	0.100	-0.060	0.296	-0.227
Grass land cover	0.206	0.118	-0.001	-0.326	-0.283	0.533
Crop land cover	0.231	0.152	-0.050	0.021	-0.023	-0.427
Wetlands	0.084	0.096	0.037	-0.399	-0.282	0.165
Water	-0.025	-0.049	-0.332	-0.017	0.013	0.225
Urban land cover	-0.009	0.169	-0.028	**0.665**	-0.187	0.229
Lake surface area	-0.102	**0.464**	-0.051	-0.158	0.170	-0.035
Dam height	-0.195	0.357	-0.143	0.067	0.119	0.009
Volume	-0.128	0.432	-0.102	-0.106	0.230	0.006
Watershed/lake surface area	-0.101	0.003	**0.558**	-0.002	0.023	0.056
Flushing index	-0.114	-0.026	0.541	-0.028	0.052	0.071
Shoreline development index	-0.125	**0.434**	-0.016	-0.117	0.100	-0.128
Chlorophyll	0.340	0.022	0.051	0.130	**0.447**	0.152
Total phosphorus	**0.373**	0.025	0.113	0.000	0.059	-0.096
Total nitrogen	0.394	0.068	0.039	0.030	0.176	0.061
Volatile solids	0.368	0.015	0.059	0.104	0.354	0.090
Non-volatile solids	0.200	0.104	0.099	-0.051	-0.373	**-0.495**
Secchi depth	-0.349	-0.117	-0.046	0.075	0.129	0.142
Conductivity	-0.034	0.269	0.166	0.434	-0.299	0.029
Percent of variation	26.8	17.6	13.8	6.9	6.3	5.5

Table 5. Regression models explaining variation in catch per effort (CPE; N/hour of electrofishing), proportional size distribution for quality size (PSD) and preferred size fish (PSD-P), and mean total length at age 3 (mm, ML3) for largemouth bass. Explanatory variables are listed in order of importance based on partial correlation coefficients. Models are listed for the reduced set of lakes for which data for all explanatory variables were available and for a larger set of lakes excluding macrophyte coverage (VEG), gizzard shad (Giz), common carp (Carp), watershed area/lake surface area ratio (WSA), and urban land cover (URBAN) variables. If these former variables were not included in the regression models for the reduced set of lakes then only models for the larger set of lakes are presented. Other explanatory variable are total phosphorus (TP), lake surface area (SA), shoreline development index (SDI), chlorophyll (CHL), non-volatile suspended solids (NVSS), and various fish variables (see Table 3 for abbreviations). Models were compared with Akaike's information criterion (AIC) for which ΔAIC indicates the difference in AIC values between the candidate model and the model with the lowest AIC value.

	Values for regression coefficients						
Explanatory variables	α	β_1	β_2	β_3	β_4	R^2	ΔAIC
	CPE (N = 111)						
BlgCPE, TP, Carp, WSA	2.850	0.598	-0.242	-0.222	-0.136	0.431	0
	CPE (N = 161)						
BlgCPE, TP	2.663	0.522	-0.236			0.270	0
	PSD (N = 111)[a]						
LmbCPE, BlgCPE, Giz, TP	0.419	-0.149	0.120	0.102	0.087	0.433	0
CHL, BlgPSD, Carp, NVSS	0.625	0.087	-0.380	0.089	0.053	0.433	0.036
CHL, Giz, BlgPSD, WSA	0.429	0.109	0.106	-0.362	0.054	0.432	0.390
LmbCPE, BlgCPE, Giz, CHL	0.633	-0.160	0.113	0.117	0.065	0.430	0.727
LmbCPE, TP, BlgCPE, SA	0.405	-0.155	0.109	0.099	0.036	0.428	0.969
	PSD (N = 161)						
TP, BlgCPE, LmbCPE, BlgPSD	0.433	0.119	0.070	-0.085	-0.224	0.318	0
BlgCPE, TP, LmbCPE, SA	0.322	0.091	0.110	-0.128	0.028	0.316	0.456
TP, LmbCPE, BlgPSD, SA	0.500	0.137	-0.052	-0.251	0.024	0.315	0.727

TP, BlgPSD, SA	0.300	0.144	-0.317	0.021		0.301	1.912
PSD-P (N = 111)							
LmbCPE, BlgCPE, Giz, NVSS	0.469	-0.193	0.136	0.079	0.068	0.511	0
PSD-P (N = 161)							
LmbCPE, BlgCPE, TP, BlgPSD	0.288	-0.129	0.079	0.113	-0.232	0.398	0
LmbCPE, BlgCPE, TP, SA	0.178	-0.172	0.100	0.104	0.027	0.393	1.511
LmbCPE, BlgCPE, TP, NVSS	0.271	-0.165	0.115	0.061	0.052	0.391	1.927
ML3 (N = 58)							
SA, BlgCPE, URBAN	136.817	10.938	23.238	-47.696		0.249	0
SA, CHL, URBAN, Giz	216.458	15.832	11.606	-51.767	-20.401	0.259	1.173
SA, BlgCPE	142.791	9.491	21.427			0.206	1.219
SA, NVSS, TP, Giz	170.341	15.979	-14.480	22.245	-18.192	0.252	1.775
ML3 (N = 83)							
SA, NVSS, TP	214.722	5.967	-8.873	13.571		0.113	0
SA, CHL	244.273	4.611	6.043			0.082	0.883
SA, TP	235.035	4.664	6.938			0.076	1.386
TP, NVSS, SDI	214.998	15.537	-9.646	15.527		0.091	1.980

[a]Only the top five models are shown. Eight more four-variable models had ΔAIC < 2.

Table 6. Regression models explaining variation in catch per effort (CPE; N/hour of electrofishing), proportional size distribution for quality size (PSD) and preferred size fish (PSD-P), and mean total length at age 3 (mm, ML3) for bluegill. Explanatory variables are listed in order of importance based on partial correlation coefficients. Models are listed for the reduced set of lakes for which data for all explanatory variables were available and for a larger set of lakes excluding macrophyte coverage (VEG), gizzard shad (Giz), common carp (Carp), watershed area/lake surface area ratio (WSA), and urban land cover (URBAN) variables. If these former variables were not included in the regression models for the reduced set of lakes then only models for the larger set of lakes are presented. Other explanatory variable are total phosphorus (TP), lake surface area (SA), shoreline development index (SDI), chlorophyll (CHL), non-volatile suspended solids (NVSS), and various fish variables (see Table 3 for abbreviations). Models were compared with Akaike's information criterion (AIC) for which ΔAIC indicates the difference in AIC values between the candidate model and the model with the lowest AIC value.

	Values for regression coefficients						
Explanatory variables	α	β_1	β_2	β_3	β_4	R^2	ΔAIC
		CPE (N = 111)					
LmbCPE, LmbPSD-P, CHL, Giz	1.637	0.588	0.878	0.134	-0.187	0.431	0
		CPE (N = 161)					
LmbCPE, LmbPSD-P, NVSS, TP	1.336	0.523	0.716	-0.179	0.299	0.383	0
		PSD (N = 111)					
LmbCPE, CHL, LmbPSD-P, BlgCPE	0.305	0.136	0.062	-0.242	-0.076	0.352	0
LmbCPE, URBAN, CHL, LmbPSD-P	0.180	0.089	0.167	0.046	-0.306	0.350	0.427
LmbCPE, CHL, LmbPSD, BlgCPE	0.305	0.153	0.064	-0.204	-0.082	0.342	1.710
LmbCPE, CHL, LmbPSD-P, Carp	0.152	0.096	0.053	-0.331	0.054	0.341	1.906

PSD (N = 161)							
LmbCPE, NVSS, BlgCPE, TP	0.145	0.167	-0.063	-0.110	0.093	0.260	0
LmbCPE, CHL, LmbPSD-P, BlgCPE	0.360	0.130	0.050	-0.174	-0.077	0.254	1.272
LmbCPE, CHL, LmbPSD, BlgCPE	0.374	0.141	0.051	-0.154	-0.082	0.250	2.000
PSD-P (N = 111)							
LmbCPE, Giz, BlgCPE, LmbPSD	-0.072	0.117	-0.075	-0.071	0.116	0.253	0
LmbCPE, NVSS, BlgCPE, LmbPSD	-0.107	0.113	-0.040	-0.061	0.121	0.246	1.023
LmbCPE, NVSS, BlgCPE, CHL	-0.034	0.098	-0.039	-0.060	0.026	0.246	1.042
LmbCPE, NVSS, BlgCPE, TP	-0.126	0.100	-0.053	-0.057	0.042	0.246	1.112
LmbCPE, Giz, BlgCPE, CHL	-0.006	0.103	-0.066	-0.066	0.019	0.245	1.274
LmbCPE, Giz, BlgCPE	0.007	0.096	-0.058	-0.053		0.231	1.319
PSD-P (N = 161)							
LmbCPE, NVSS, BlgCPE, TP	-0.075	0.099	-0.056	-0.065	0.041	0.249	0
LmbCPE, NVSS, BlgCPE, CHL	0.012	0.093	-0.046	-0.063	0.027	0.247	0.288
ML3 (N = 62)							
LmbPSD-P, CHL, Giz, Carp	140.934	-47.925	6.485	-14.426	8.028	0.358	0
LmbPSD-P, Giz, CHL	143.078	-41.496	-11.245	5.551		0.316	1.984
ML3 (N = 86)							
LmbPSD-P, CHL	138.559	-52.832	5.399			0.214	0

Table 7. Regression models explaining variation in catch per effort (CPE; N/hour of electrofishing), proportional size distribution for quality size (PSD) and preferred size fish (PSD-P), and mean total length at age 3 (mm, ML3) for redear sunfish. Explanatory variables are listed in order of importance based on partial correlation coefficients. Models are listed for the reduced set of lakes for which data for all explanatory variables were available and for a larger set of lakes excluding macrophyte coverage (VEG), gizzard shad (Giz), common carp (Carp), watershed area/lake surface area ratio (WSA), and urban land cover (URBAN) variables. If these former variables were not included in the regression models for the reduced set of lakes then only models for the larger set of lakes are presented. Other explanatory variable are total phosphorus (TP), lake surface area (SA), shoreline development index (SDI), chlorophyll (CHL), non-volatile suspended solids (NVSS), and various fish variables (see Table 3 for abbreviations). Models were compared with Akaike's information criterion (AIC) for which ΔAIC indicates the difference in AIC values between the candidate model and the model with the lowest AIC value. The maximum number of explanatory variables was restricted to three for ML3 models due to small sample sizes.

	Values for regression coefficients						
Explanatory variables	α	β_1	β_2	β_3	β_4	R^2	ΔAIC
CPE (N = 55)							
LmbPSD, VEG, BlgCPE, SDI	2.103	-2.143	0.520	0.606	-0.616	0.341	0
LmbPSD, VEG, BlgCPE, URBAN	1.327	-2.185	0.587	0.717	-1.546	0.338	0.271
BlgCPE, LmbPSD-P, SDI, LmbCPE	4.819	0.881	-3.201	-0.786	-0.903	0.327	1.147
LmbPSD, BlgCPE, SDI, TP	3.177	-1.459	0.637	-0.879	-0.348	0.325	1.289
LmbPSD, BlgCPE, SDI, CHL	2.208	-1.692	0.759	-0.838	-0.283	0.325	1.300
LmbPSD, VEG, BlgCPE, SA	1.959	-2.192	0.488	0.652	-0.161	0.324	1.397
LmbPSD, BlgCPE, SDI, LmbCPE	4.637	-2.346	0.786	-0.805	-0.650	0.324	1.427
LmbPSD, VEG, BlgCPE, TP	2.098	-2.029	0.587	0.667	-0.243	0.322	1.524
LmbPSD, VEG, BlgCPE	1.567	-2.396	0.608	0.645		0.296	1.595

CPE (N = 72)							
LmbPSD, CHL, BlgCPE, SDI	1.930	-1.581	-0.319	0.757	-0.515	0.211	0
LmbPSD-P, CHL, BlgCPE, SDI	1.459	-1.963	-0.332	0.785	-0.519	0.207	0.353
LmbPSD, BlgCPE, TP, SDI	2.925	-1.394	0.632	-0.375	-0.528	0.206	0.464
LmbPSD, BlgCPE, CHL	1.671	-1.701	0.723	-0.289		0.182	0.624
LmbPSD-P, BlgCPE, CHL	1.161	-2.115	0.752	-0.302		0.177	1.008
LmbPSD, BlgCPE, TP	2.549	-1.547	0.607	-0.329		0.175	1.185
PSD (N = 72)							
RedCPE, TP, SA, LmbPSD-P	0.932	-0.108	0.112	0.047	-0.468	0.334	0
RedCPE, CHL, SA, BlgCPE	1.496	-0.088	0.095	0.040	-0.130	0.331	0.271
RedCPE, CHL, SA, LmbPSD-P	1.129	-0.112	0.081	0.040	-0.386	0.329	0.486
RedCPE, CHL, BlgCPE	1.559	-0.097	0.092	-0.108		0.305	1.042
RedCPE, CHL, LmbPSD-P	1.251	-0.117	0.080	-0.316		0.302	1.307
RedCPE, TP, LmbPSD-P	1.104	-0.115	0.102	-0.369		0.298	1.774
PSD-P (N = 72)							
RedCPE, LmbCPE, CHL, BlgCPE	0.290	-0.103	0.215	0.081	-0.133	0.358	0
RedCPE, LmbCPE, CHL, LmbPSD-P	0.167	-0.126	0.153	0.072	-0.384	0.353	0.549
RedCPE, LmbCPE, TP, LmbPSD-P	-0.087	-0.124	0.181	0.090	-0.413	0.351	0.785
RedCPE, LmbCPE, TP, BlgCPE	-0.011	-0.105	0.241	0.077	-0.105	0.341	1.846
ML3 (N = 22)							
CHL, SA, LmbPSD	128.346	14.315	12.033	-52.564		0.528	0
CHL, SA, LmbPSD-P	114.484	13.775	12.324	-62.253		0.501	1.212
CHL, Carp, SA	105.076	10.316	14.443	10.138		0.490	1.696
ML3 (N = 28)							
TP, SA, LmbPSD-P	103.178	18.665	9.421	-91.996		0.287	0

SDI, CHL	124.058	27.405	9.411			0.224	0.367
CHL, SA, LmbPSD-P	131.860	11.831	8.929	-65.592		0.264	0.909
TP, SDI, LmbPSD-P	112.722	17.227	23.140	-71.120		0.260	1.063
SDI	150.910	23.661				0.126	1.694

Table 8. Regression models explaining variation in catch per effort (CPE; N/hour of electrofishing), proportional size distribution for quality size (PSD) and preferred size fish (PSD-P), and mean total length at age 3 (mm, ML3) for white crappie. Explanatory variables are listed in order of importance based on partial correlation coefficients. Models are listed for the reduced set of lakes for which data for all explanatory variables were available and for a larger set of lakes excluding macrophyte coverage (VEG), gizzard shad (Giz), common carp (Carp), watershed area/lake surface area ratio (WSA), and urban land cover (URBAN) variables. If these former variables were not included in the regression models for the reduced set of lakes then only models for the larger set of lakes are presented. Other explanatory variable are total phosphorus (TP), lake surface area (SA), shoreline development index (SDI), chlorophyll (CHL), non-volatile suspended solids (NVSS), and various fish variables (see Table 3 for abbreviations). Models were compared with Akaike's information criterion (AIC) for which ΔAIC indicates the difference in AIC values between the candidate model and the model with the lowest AIC value. The maximum number of explanatory variables was restricted to three for ML3 models due to small sample sizes.

	Values for regression coefficients						
Explanatory variables	α	β_1	β_2	β_3	β_4	R^2	ΔAIC
		CPE (N = 67)					
NVSS, Giz, BlgCPE	-0.254	0.629	0.823	0.399		0.364	0
Giz, NVSS, SA, SDI	1.468	0.647	0.542	0.385	-1.012	0.378	0.557
NVSS, Giz, SA	1.376	0.581	0.605	0.138		0.350	1.434
		CPE (N = 94)					
NVSS, SA, BlgCPE, LmbCPE	1.056	0.594	0.169	0.506	-0.402	0.311	0
NVSS, LmbPSD-P, SA, BlgCPE	0.239	0.588	0.849	0.145	0.262	0.311	0.015
NVSS, LmbPSD-P, SA	1.506	0.563	0.860	0.152		0.296	0.040
NVSS, LmbPSD-P, BlgCPE, CHL	0.726	0.704	0.900	0.399	-0.272	0.303	1.064
NVSS, LmbPSD-P, TP, BlgCPE	1.406	0.817	1.003	-0.385	0.365	0.301	1.354

NVSS, SA, BlgCPE	0.484	0.678	0.145	0.268		0.283	1.736
NVSS, SA	1.784	0.654	0.152			0.267	1.775
PSD (N = 67)							
BlgCPE , WhcCPE, LmbCPE, LmbPSD-P	1.059	-0.290	-0.116	0.304	0.454	0.288	0
BlgCPE , WhcCPE, LmbCPE, URBAN	1.532	-0.265	-0.101	0.222	-0.345	0.276	1.089
BlgCPE , WhcCPE, LmbCPE, VEG	1.427	-0.262	-0.096	0.210	0.144	0.274	1.246
BlgCPE , WhcCPE, LmbCPE, LmbPSD	1.092	-0.287	-0.105	0.272	0.338	0.271	1.513
BlgCPE , WhcCPE, LmbCPE	1.464	-0.268	-0.101	0.222		0.247	1.709
PSD (N = 94)							
BlgCPE , WhcCPE, LmbCPE, LmbPSD-P	0.796	-0.223	-0.105	0.289	0.346	0.244	0
BlgCPE , WhcCPE, LmbCPE, LmbPSD	0.740	-0.214	-0.096	0.267	0.306	0.241	0.486
PSD-P (N = 67)							
SA, LmbCPE, BlgCPE, WhcCPE	0.304	0.072	0.187	-0.168	-0.064	0.287	0
LmbCPE, BlgCPE, SA, Carp	0.247	0.199	-0.188	0.066	-0.116	0.267	1.817
LmbCPE, BlgCPE, SDI, WhcCPE	0.283	0.171	-0.144	0.215	-0.053	0.266	1.917
PSD-P (N = 94)							
LmbCPE, BlgCPE, LmbPSD, WhcCPE	-0.057	0.221	-0.126	0.292	-0.042	0.215	0
LmbCPE, BlgCPE, LmbPSD	-0.166	0.245	-0.148	0.269		0.188	1.215
ML3 (N = 34)							
WhcCPE, LmbPSD-P, SDI	250.064	-11.417	-59.432	24.586		0.477	0
WhcCPE, CHL, SDI	202.977	-16.317	12.748	23.976		0.457	1.283
WhcCPE, LmbPSD, SDI	264.928	-13.596	-43.368	24.721		0.451	1.675

Table 9. Regression models explaining variation in catch per effort (CPE; N/hour of electrofishing), proportional size distribution for quality size (PSD) and preferred size fish (PSD-P), and mean total length at age 3 (mm, ML3) for black crappie. Explanatory variables are listed in order of importance based on partial correlation coefficients. Models are listed for the reduced set of lakes for which data for all explanatory variables were available and for a larger set of lakes excluding macrophyte coverage (VEG), gizzard shad (Giz), common carp (Carp), watershed area/lake surface area ratio (WSA), and urban land cover (URBAN) variables. If these former variables were not included in the regression models for the reduced set of lakes then only models for the larger set of lakes are presented. Other explanatory variable are total phosphorus (TP), lake surface area (SA), shoreline development index (SDI), chlorophyll (CHL), non-volatile suspended solids (NVSS), and various fish variables (see Table 3 for abbreviations). Models were compared with Akaike's information criterion (AIC) for which ΔAIC indicates the difference in AIC values between the candidate model and the model with the lowest AIC value. The maximum number of explanatory variables was restricted to two for ML3 models due to small sample sizes.

	Values for regression coefficients						
Explanatory variables	α	β_1	β_2	β_3	β_4	R^2	ΔAIC
CPE (N = 60)							
LmbPSD, LmbCPE	-0.175	1.164	0.408			0.113	0
LmbPSD	1.590	1.217				0.078	0.288
PSD (N = 44)							
BlcCPE, LmbCPE, VEG, WSA	0.546	-0.132	0.241	0.153	-0.131	0.301	0
BlcCPE, LmbCPE, WSA, SDI	0.241	-0.137	0.306	-0.153	0.163	0.291	0.652
BlcCPE, LmbCPE, WSA	0.518	-0.130	0.279	-0.160		0.257	0.670
BlcCPE, LmbCPE, VEG	0.163	-0.122	0.232	0.189		0.255	0.814
BlcCPE, VEG	1.191	-0.126	0.218			0.200	1.957
PSD (N = 60)							
BlgCPE	1.237	-0.122				0.106	0
PSD-P (N = 44)							

Giz, BlcCPE, WSA	1.190	-0.253	-0.083	-0.140		0.253	0
Giz, LmbPSD-P, WSA	1.156	-0.252	-0.453	-0.134		0.243	0.581
Giz, WSA	0.962	-0.289	-0.125			0.206	0.646
Giz	0.594	-0.286				0.160	1.128
PSD-P (N = 60)							
CHL, BlcCPE, SA, LmbPSD	0.272	0.136	-0.073	0.058	-0.433	0.148	0
BlcCPE, LmbCPE	-0.174	-0.085	0.175			0.085	0.288
CHL, LmbPSD, SA	0.181	0.133	-0.507	0.051		0.110	0.611
CHL, BlcCPE, SA, LmbPSD-P	0.204	0.116	-0.077	0.053	-0.406	0.133	1.036
CHL, LmbPSD	0.362	0.105	-0.393			0.072	1.128
BlcCPE	0.560	-0.069				0.037	1.333
LmbCPE	-0.218	0.137				0.030	1.753
ML3 (N = 11)							
Carp, BlgCPE	570.211	-55.767	-62.096			0.723	0
SDI, WSA	78.686	-62.340	72.620			0.704	0.708
SA, WSA	189.578	-22.276	45.378			0.687	1.344
ML3 (N = 15)							
LmbPSD-P	257.440	-77.606				0.167	0
BlgCPE, LmbCPE	376.815	-53.722	26.320			0.271	0.007
LmbPSD	267.330	-53.472				0.164	0.050
BlgCPE	417.537	-38.493				0.159	0.153
SA	262.902	-8.755				0.119	0.845
SDI	248.042	-20.892				0.073	1.604
BlcCPE	255.716	-10.560				0.070	1.650

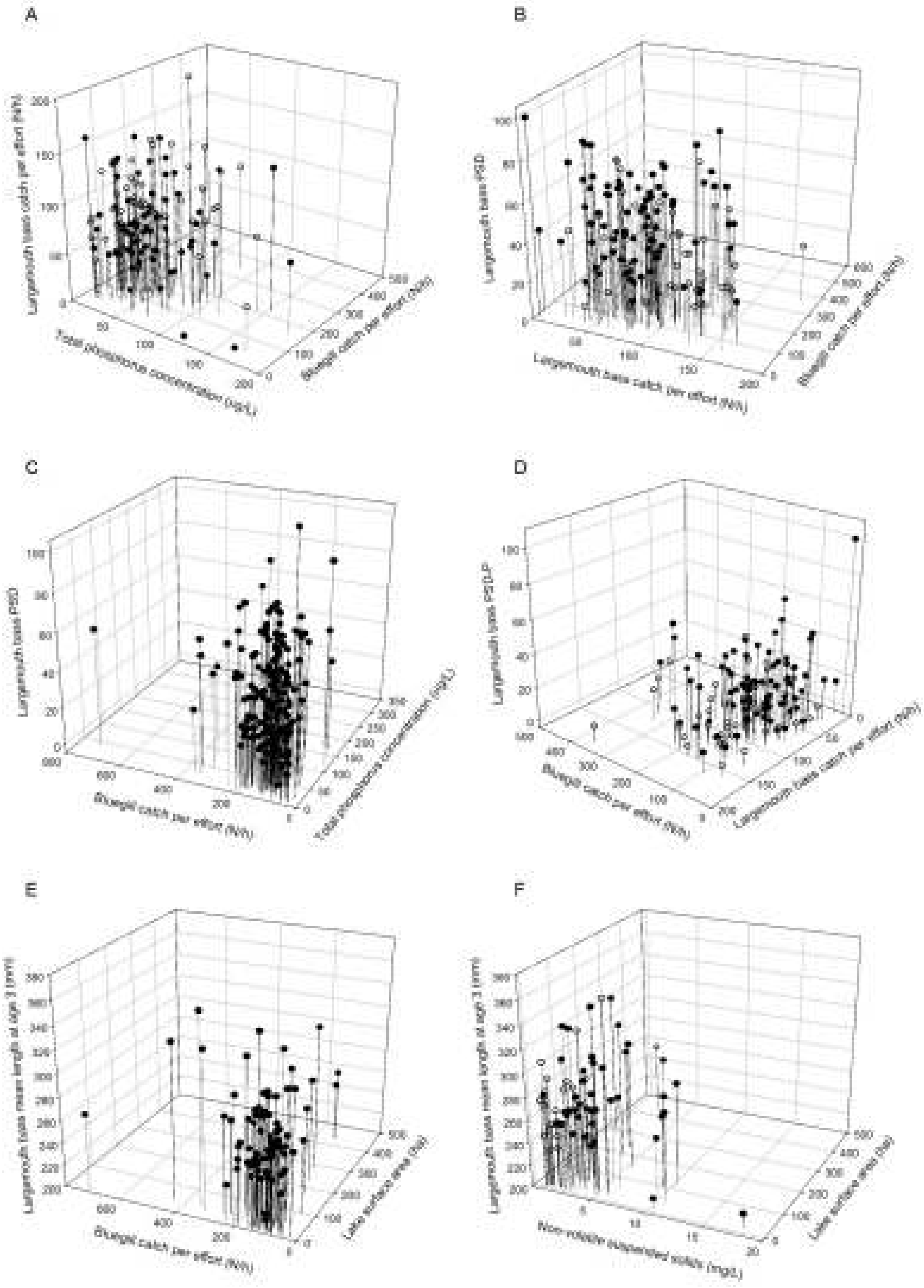
Figure 1. Scatterplots showing relationships among explanatory variables and largemouth bass catch per unit effort (panel A), proportional stock density (PSD, panels B and C), PSD of quality size fish (PSD-P, panel D), and mean length at age 3 (panels E and F). All variables are untransformed for ease of interpretation. For panel A, filled circles indicate lakes with common carp and open circles indicate lakes without common carp. For panels B, D, and F, filled circles indicate lakes with gizzard shad and open circles indicate lakes without gizzard shad.

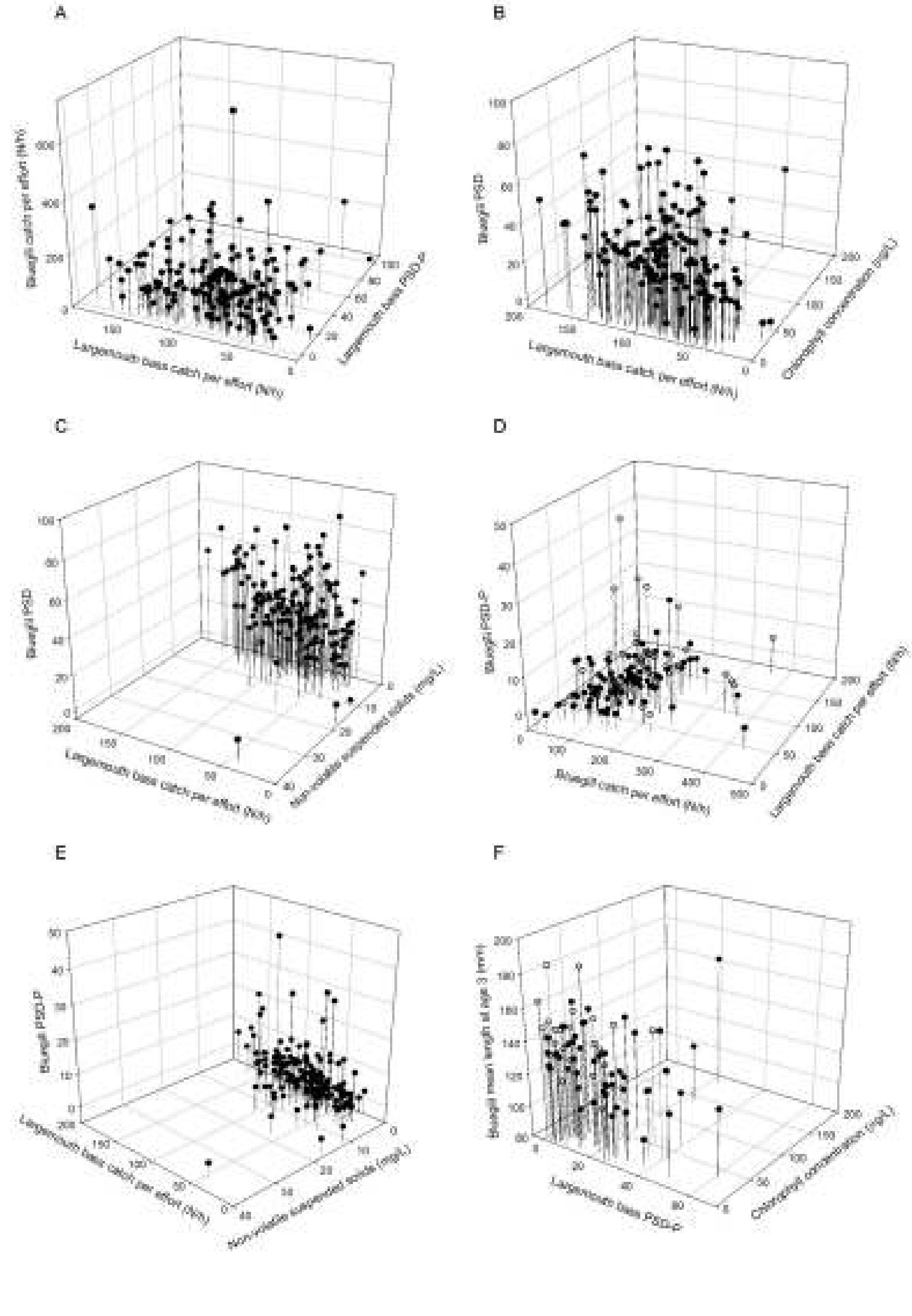
Figure 2. Scatterplots showing relationships among explanatory variables and bluegill catch per unit effort (panel A), proportional stock density (PSD, panels B and C), PSD of quality size fish (PSD-P, panels D and E), and mean length at age 3 (panel F). All variables are untransformed for ease of interpretation. For panels D and F, filled circles indicate lakes with gizzard shad and open circles indicate lakes without gizzard shad.

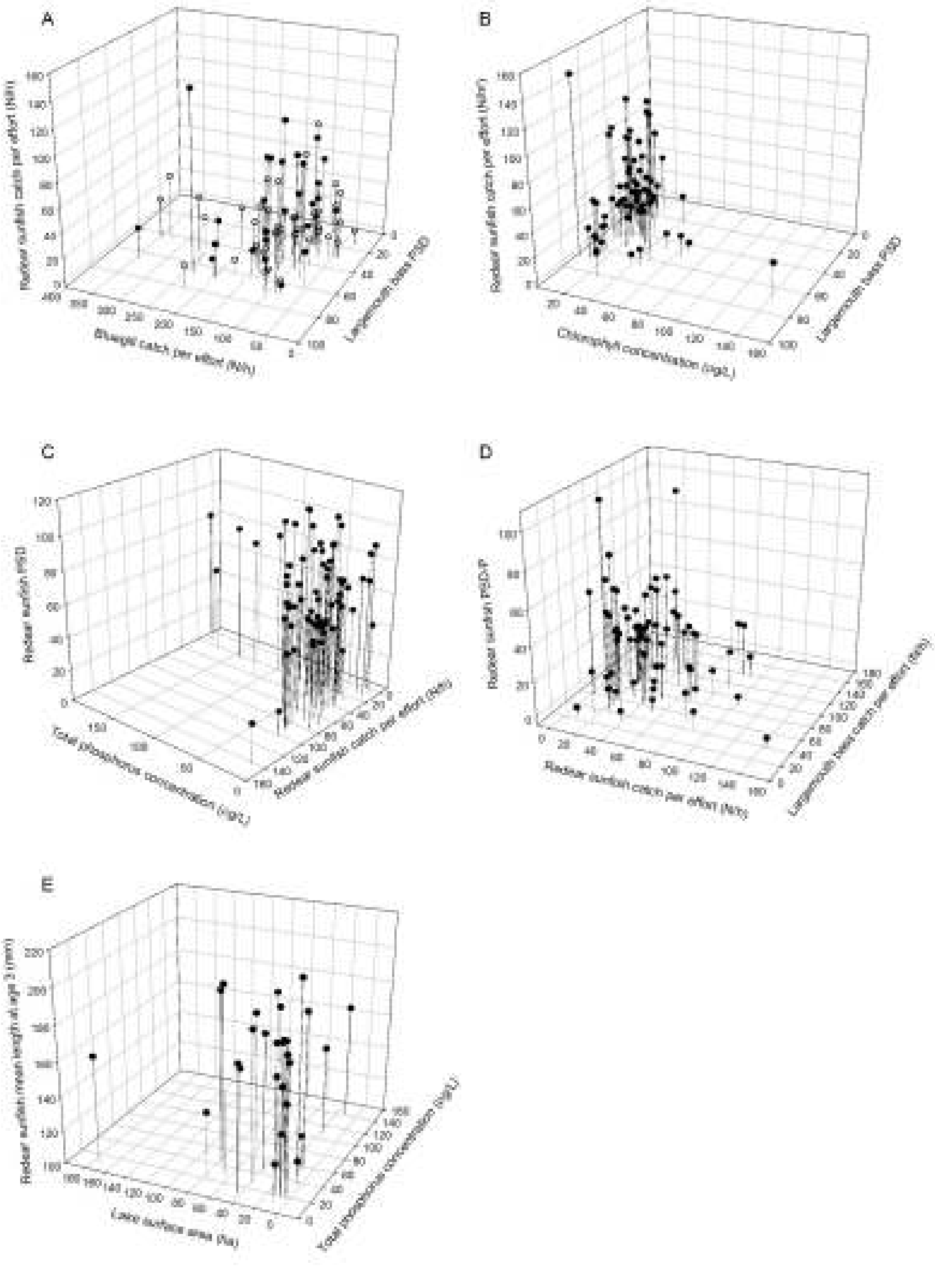
Figure 3. Scatterplots showing relationships among explanatory variables and redear sunfish catch per unit effort (panels A and B), proportional stock density (PSD, panel C), PSD of quality size fish (PSD-P, panel D), and mean length at age 3 (panel E). All variables are untransformed for ease of interpretation. For panel A, filled circles indicate lakes with abundant vegetation and open circles indicate lakes sparse vegetation.

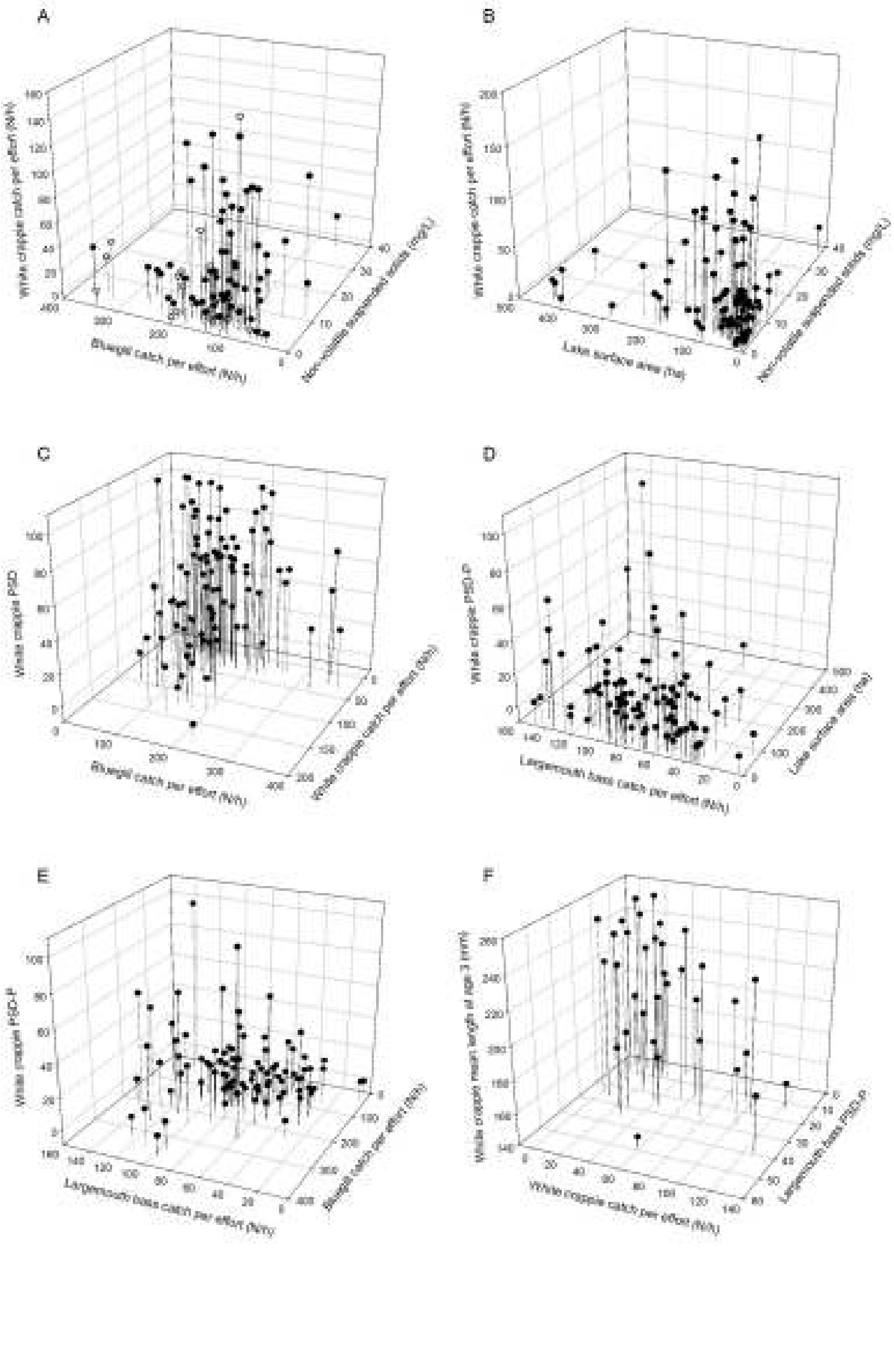
Figure 4. Scatterplots showing relationships among explanatory variables and white crappie catch per unit effort (panels A and B), proportional stock density (PSD, panel C), PSD of quality size fish (PSD-P, panels D and E), and mean length at age 3 (panel F). All variables are untransformed for ease of interpretation. For panel A, filled circles indicate lakes with gizzard shad and open circles indicate lakes without gizzard shad.

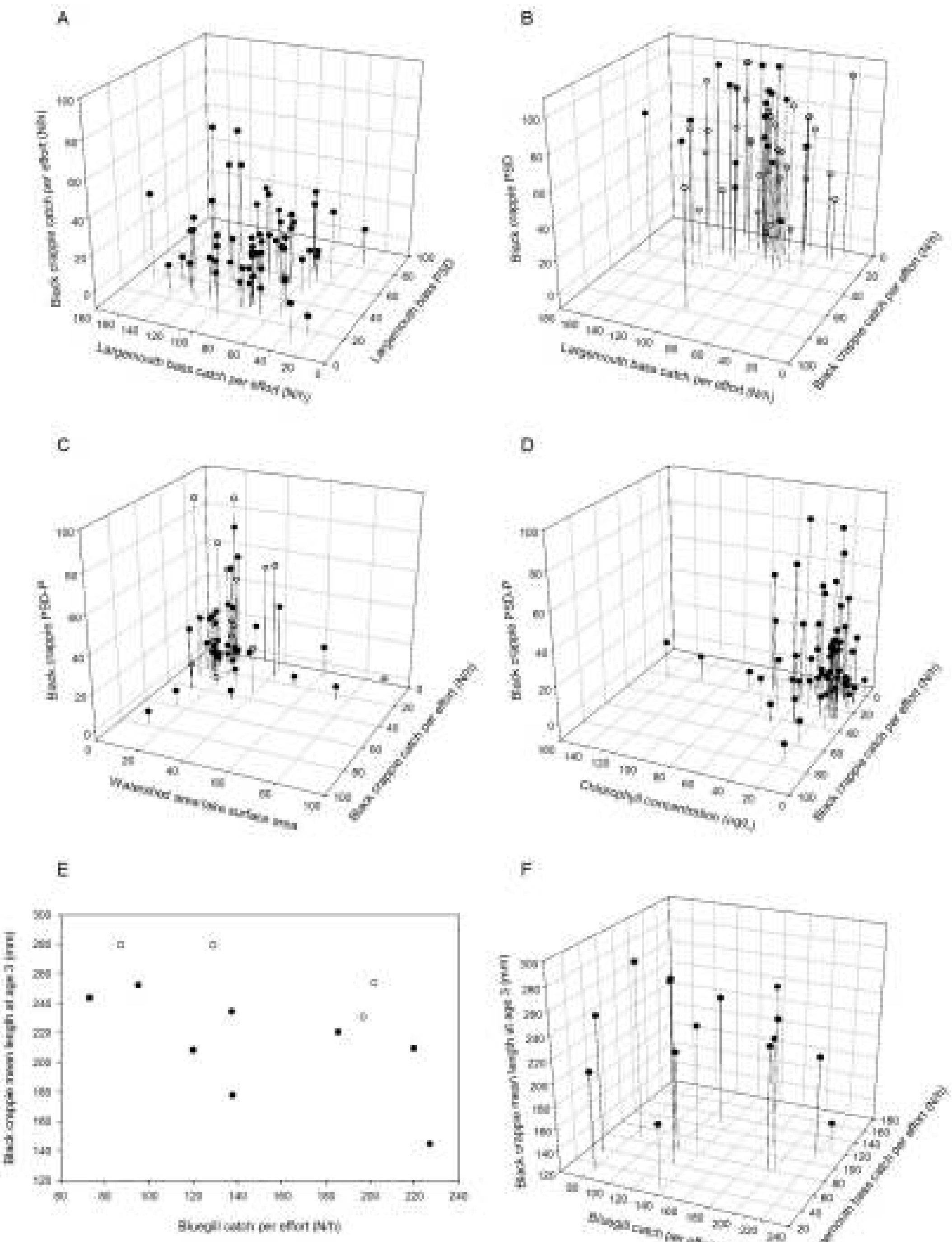
Figure 5. Scatterplots showing relationships among explanatory variables and black crappie catch per unit effort (panel A), proportional stock density (PSD, panel B), PSD of quality size fish (PSD-P, panels C and D), and mean length at age 3 (panels E and F). All variables are untransformed for ease of interpretation. For panel B, filled circles indicate lakes with abundant vegetation and open circles indicate lakes sparse vegetation. For panel C, filled circles indicate lakes with gizzard shad and open circles indicate lakes without gizzard shad. For panel E, filled circles indicate lakes with common carp and open circles indicate lakes without common carp.


A
Largemouth bass catch per effort (N/h)
Total phosphorus concentration (ug/L)
Bluegill catch per effort (N/h)
B
Largemouth bass PSD
Largemouth bass catch per effort (N/h)
Bluegill catch per effort (N/h)
C
Largemouth bass PSD
Bluegill catch per effort (N/h)
Total phosphorus concentration (ug/L)
D
Largemouth bass PSD-P
Bluegill catch per effort (N/h)
Largemouth bass catch per effort (N/h)
E
Largemouth bass mean length at age 3 (mm)
Bluegill catch per effort (N/h)
Lake surface area (ha)
F
Largemouth bass mean length at age 3 (mm)
Non-volatile suspended solids (mg/L)
Lake surface area (ha)


A
Bluegill catch per effort (N/h)
Largemouth bass catch per effort (N/h)
Largemouth bass PSD-P
B
Bluegill PSD
Largemouth bass catch per effort (N/h)
Chlorophyll concentration (mg/L)
C
Bluegill PSD
Largemouth bass catch per effort (N/h)
Nonvolatile suspended solids (mg/L)
D
Bluegill PSD-P
Bluegill catch per effort (N/h)
Largemouth bass catch per effort (N/h)
E
Bluegill PSD-P
Largemouth bass catch per effort (N/h)
Nonvolatile suspended solids (mg/L)
F
Bluegill mean length at age 3 (mm)
Largemouth bass PSD-P
Chlorophyll concentration (mg/L)


A
Redear sunfish catch per effort (N/h)
Bluegill catch per effort (N/h)
Largemouth bass PSD
B
Redear sunfish catch per effort (N/h)
Chlorophyll concentration
Largemouth bass PSD
C
Redear sunfish PSD
Total phosphorus concentration
Redear sunfish catch per effort (N/h)
D
Redear sunfish PSD-P
Redear sunfish catch per effort (N/h)
Largemouth bass catch per effort (N/h)
E
Redear sunfish mean length at age 3 (mm)
Lake surface area (ha)
Total phosphorus concentration


A
White crappie catch per effort (N/h)
Bluegill catch per effort (N/h)
Non-volatile suspended solids (mg/L)
B
White crappie catch per effort (N/h)
Lake surface area (ha)
Non-volatile suspended solids (mg/L)
C
White crappie PSD
Bluegill catch per effort (N/h)
White crappie catch per effort (N/h)
D
White crappie PSD-P
Largemouth bass catch per effort (N/h)
Lake surface area (ha)
E
White crappie PSD-P
Largemouth bass catch per effort (N/h)
Bluegill catch per effort (N/h)
F
White crappie mean length at age 3 (mm)
White crappie catch per effort (N/h)
Largemouth bass PSD-P


A
Black crappie catch per effort (N/h)
Largemouth bass catch per effort (N/h)
Largemouth bass PSD
B
Black crappie PSD
Largemouth bass catch per effort (N/h)
Black crappie catch per effort (N/h)
C
Black crappie PSD-P
Watershed area:lake surface area
Black crappie catch per effort (N/h)
D
Black crappie PSD-P
Black crappie catch per effort (N/h)
E
Black crappie mean length at age 3 (mm)
Bluegill catch per effort (N/h)
F
Black crappie mean length at age 3 (mm)
Bluegill catch per effort (N/h)
Largemouth bass catch per effort (N/h)