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Common carp (*Cyprinus carpio*), sport fishes, and water quality: Ecological thresholds in agriculturally eutrophic lakes

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Abstract

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We examined fish populations, limnological conditions, lake basin morphology and watershed characteristics to evaluate patterns in population characteristics of ecologically important fish species in relation to environmental conditions in agriculturally eutrophic lake systems. Fish populations and environmental characteristics were sampled from 129 Iowa lakes using standard techniques from 2001–2006. Lakes with high catch rates of common carp (*Cyprinus carpio*) had high nutrient concentrations, high phytoplankton biomass and low water transparency. In addition, lakes with high catch rates of common carp had low catch rates of important sport fishes including bluegill (*Lepomis macrochirus*), largemouth bass (*Micropterus salmoides*), black crappie (*Pomoxis nigromaculatus*) and white crappie (*P. annularis*). The relationship between common carp and sport fishes appeared to function as an ecological threshold. Specifically, when common carp catch rates were >2 kilograms per fyke net night, catch rates of sport fish were always low and water quality in the study lakes was poor. Shallow systems (natural lakes, oxbows) had higher densities of common carp compared to deeper systems (impoundments, surface mines), thereby suggesting that shallow lakes are most sensitive to the effects of common carp and that restoration efforts incorporating biomanipulation of common carp will likely be most successful in shallow systems.

Key words: alternative stable states, ecological thresholds, eutrophication, water quality

A common view among aquatic ecologists is that nutrient-rich lakes generally exist in 1 of 2 alternate stable states: one where the lake is clear with abundant submerged plants (clear-water state) or one where the lake has low light penetration and little or no aquatic vegetation (turbid-water state; Scheffer et al. 1993). A number of factors, acting individually or in concert, may influence whether a lake is in a clear or turbid state (Scheffer 1998). One factor, benthivorous fishes, has direct and indirect effects on lakes and may be a major determinant of whether a lake is in a clear or turbid state. Benthivorous fishes feed by rummaging through sediments, filtering food items and expelling sediment into the water column (Breukelaar et al. 1994). Through these mechanisms, benthivorous fish reduce the abundance and diversity of benthos communities (Miller and Crowl 2006), and many benthivores directly consume roots and other tissues of aquatic macrophytes (Ten Winkel and Meulemans 1984). Indirect effects of benthivores are also important in regulating the state of a lake, where resuspension of nutrients and sediment from benthic habitats to the water column may yield the same response as high external inputs of nutrients and sediment (Tatrai et al. 2009). High densities of nonnative, benthivorous common carp (*Cyprinus carpio*) have been associated with the degradation of habitat conditions in lakes across Canada, the United States and Mexico (Lougheed et al. 1998, Zambrano et al. 1999). Given their influence on aquatic ecosystems, common carp have been the target of extensive removal programs in both lentic (Schrage and Downing 2004) and lotic (Verrill and Berry 1995) habitats to improve water quality and biological communities.

Changes in the state of a system also have dramatic effects on fish assemblage structure. Fish assemblages in turbid

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lakes are often dominated by benthivores and contain few sight-feeding predators, whereas lakes in a clear state often contain a diversity and abundance of sight-feeding predators (Breukelaar et al. 1994, Jeppesen et al. 2000). Nearly all popular sport fishes in North America, such as walleye (*Sander vitreus*), bluegill (*Lepomis macrochirus*) and black bass (*Micropterus* spp.) are sight-feeding predators. If a lake switches from a clear to a turbid state, consequent changes in the abundance and population structure of these fishes may greatly alter food web ecology as well as local economies that rely on income from recreational angling.

This study was conducted in Iowa, one of the world's most agricultural regions (Downing et al. 1999). Like most states in the central United States, Iowa is faced with substantial water quality issues, primarily those related to high nutrient and sediment inputs (Arbuckle and Downing 2001). Of the 243 public lakes in Iowa, 132 have been identified by the Iowa Department of Natural Resources (IDNR) as "principal recreation lakes." Over half (~55%) of the 132 lakes are on the U.S. Environmental Protection Agency's 2006 list of impaired waters (IDNR 2008a). Moreover, when asked about factors limiting recreation, Iowa anglers identify poor water quality as the second most important reason for not spending more time angling in Iowa (IDNR 2008b).

Although high nutrient and sediment inputs, coupled with widespread occurrence of common carp, are considered to be the primary cause of poor water quality and poor sport fish populations, little research has been conducted over a large spatial scale to elucidate important factors influencing lake systems in such highly agricultural landscapes. The objective of this study was to describe relationships among common carp, sport fishes and limnological characteristics in Iowa lakes and provide guidance for management. We hypothesized that lakes with high densities of common carp would have poor water quality and low densities of important sport fishes.

Materials and methods

Data were collected from 129 of Iowa's principal recreation lakes during 2001–2006. Lakes were defined broadly as natural lakes, impoundments, mines (abandoned gravel pits) and oxbow lakes. Fish were sampled using standard methods including DC electrofishing and modified fyke nets (IDNR 1995). Boat electrofishing was conducted during the day in 15-min runs. Guidelines for electrofishing were 30–90 min of electrofishing in lakes <40 ha, 60–120 min in lakes 40–200 ha, and >90 min in lakes >200 ha. Fyke nets (12.2 m lead, two 0.6 m × 1.2 m frames, seven 0.6-m dia hoops; 19-mm bar measure mesh) were fished overnight and processed the following day (i.e., a net night [NN]). Guidelines for fyke net sampling were 3–15 net nights in lakes <40 ha, 5–20 net nights in lakes 40–200 ha, and 7–28 net nights in lakes >200 ha.

Sampling was conducted during September–October; however, supplemental sampling in the spring was conducted in some lakes to obtain additional structures for age and growth analysis. The analysis focused on 4 important sport fish species: bluegill, largemouth bass (*Micropterus salmoides*), black crappie (*Pomoxis nigromaculatus*), white crappie (*P. annularis*) and common carp. Not only are these species important from social and ecological perspectives (IDNR 2008b), but they were typically the only species consistently sampled across all lakes.

A minimum of 50 stock-length or longer fish of each target species from each lake were measured to the nearest 2.5 mm and weighed to the nearest gram. Stock lengths were 280 mm for common carp, 80 mm for bluegill, 200 mm for largemouth bass, and 130 mm for black crappie and white crappie (Anderson and Neumann 1996). Additional fish were counted. Structures were collected from fish for age and growth analysis following standard methods (DeVries and Frie 1996). Scales were used to age all fish except for common carp, which were aged using dorsal spines.

Measures of dissolved oxygen, nutrients, pH, suspended solids, turbidity, specific conductivity, chlorophyll *a*, alkalinity and silica were measured for each lake (Downing et al. 2005). Water samples, collected between mid-May and mid-August 3 times per year, were used to estimate broad patterns of water quality among lakes (Downing et al. 2005). Integrated samples of the epilimnion, or of the entire water column in the absence of a thermocline, were processed and analyzed using standard methods; specific analytical techniques can be found in Egertson and Downing (2004). Although water samples were obtained earlier in the year than fish samples, we were primarily interested in broad patterns of water quality among lakes. Moreover, May–August sampling provides an excellent characterization of water quality in Iowa lakes (Downing et al. 2005). Watershed characteristics, including the ratio of watershed area to lake surface area and percent of the watershed as row-crop agriculture, were calculated using IDNR land-use data (M. Hawkins, IDNR, unpublished data).

Summary statistics (mean, median, variance, minimum, maximum) were calculated to provide a description of fish populations in the study lakes. Catch-per-unit-effort (CPUE) was estimated as the number of bluegill, black crappie and white crappie sampled per fyke net night and the number of largemouth bass per hour of electrofishing. Estimates of relative abundance for common carp were calculated as kilograms of fish caught per fyke net night. Catch rates for common carp were also examined by number, but patterns were nearly identical to those observed using weight-based catch rates. In addition, using CPUE by weight is consistent with previous investigations in these lakes and is commonly used by IDNR to evaluate common carp populations (Egertson and Downing 2004). Size structure was assessed for each population by calculating proportional size distribution (PSD = 100 × [number of fish of quality length or larger/number of fish of stock length or larger]; Anderson and Neumann 1996). Quality lengths were 410 mm for common carp, 150 mm for bluegill, 300 mm for largemouth bass and 200 mm for black crappie and white crappie. Body condition was evaluated for individual fish in each population using relative weight ($Wr = 100 \times$ [observed weight/length-specific standard weight]; Anderson and Neumann 1996).

Growth rates of fishes sampled from the study lakes were also described. Age and growth was estimated using standard processing and analysis techniques (DeVries and Frie 1996). The Fraser-Lee method was used to estimate mean back-calculated length at age for fish aged with scales using standard-intercept values provided by Carlander (1982). Mean back-calculated length at age for common carp was estimated using the Dahl-Lea method (DeVries and Frie 1996). Populations in which fewer than 30 individuals were collected were removed from the growth analysis. Summary statistics included mean back-calculated length at age and mean relative growth index (RGI = 100 × [observed length/age-specific standard length]; Jackson et al. 2008).

Relationships of common carp catch rates with bluegill, largemouth bass, black crappie and white crappie abundance were first investigated by plotting catch rates of common carp against catch rates of the four other study species. Bivariate plots indicated that common carp and the other species were not linearly related; rather, the relationships seemed to function as threshold responses. Therefore, a 2-dimensional Kolmogorov-Smirnov (2DKS) test was used to test patterns and identify thresholds of abundance (Garvey et al. 1998). The 2DKS test compares the observed joint distribution of abundances to a distribution expected if abundances occurred independently. The test is based on a test statistic, D, that is a measure of departure between the observed and expected distributions. The significance of each test was evaluated using a permutation test, where the proportion of randomly-generated Ds (from 5000 rerandomizations of the observed x, y pairs) exceeding the observed D-statistic was determined. If the proportion exceeded 0.05 ($P > 0.05$), we concluded that the observed pattern was due to chance. The 2DKS test also provides the threshold (x, y pair), or maximum point of departure, within each distribution. For each bivariate plot, threshold catch rates were used to categorize lakes as belonging to 1 of 2 catch rate categories: (1) high CPUE of common carp, low CPUE of bluegill, largemouth bass, black crappie or white crappie (hereafter referred to as high carp–low sport fish species); (2) low CPUE of common carp, high CPUE of bluegill, largemouth bass, black crappie, or white crappie (hereafter referred to as low carp–high sport fish species).

Many of the water quality, lake basin morphology, watershed land use and fish population variables were correlated ($P \leq 0.05$); therefore, variables were selected to ensure at least one variable from each category (lake basin morphology, watershed land use, water quality, fish population characteristics) was included in the analysis. In addition, several water quality variables were included in the analysis due to their regulatory or management importance (e.g., nutrient and cyanobacteria concentrations). The 10 variables selected for further investigation were watershed to lake area ratio; percentage of row-crop agriculture in the watershed; mean depth; concentrations of total suspended solids, chlorophyll a, cyanobacteria, total phosphorus and total nitrogen; Secchi disk transparency; and RGI values. Because not all of the variables were normally distributed (Shapiro-Wilks test; $P = 0.0001$–0.06 among variables), a nonparametric Mann-Whitney test was used to evaluate whether environmental and population dynamics variables differed between the 2 catch rate categories (Sokal and Rohlf 1995). Analyses were conducted using SAS (SAS Institute 1996).

Fish population characteristics were further examined using nonmetric multidimensional scaling (NMDS), a multivariate technique that summarizes data by producing a low-dimensional ordination space where lakes with similar fish population characteristics (e.g., catch rates of fishes) are plotted near each other, and those with dissimilar characteristics are positioned apart (McCune and Mefford 2006). Sorenson distance measure and random starting configurations were used for the NMDS analyses. The number of dimensions was determined when reductions in stress diminished with additional axes. Pearson correlations were used to evaluate associations between fish population characteristics (NMDS scores), water quality, lake morphology and watershed data. The NMDS analysis was conducted using PC-ORD (McCune and Mefford 2006).

Results

Study lakes varied in surface area from 4 to 2174 ha, had watershed to lake area ratios from <0.5 to about 290 and mean depths from about 1 to 12 m (Table 1). Nutrient concentrations and percent of the watershed in row-crop agriculture were generally high (total phosphorus $\geq$ 100 ug/L, row-crop > 40%), and Secchi transparency was typically low (<1.5 m) across study lakes. Samples included 113,103 fish representing 10 families and 44 species. The study species accounted for the majority (68%) of all fish

Table 1.-Physicochemical habitat and fish population characteristics sampled from 129 Iowa lakes, 2001–2006. Mean, median, standard deviation (SD), minimum (Min) and maximum (Max) values are provided as an indication of the variation among lakes.

Variables	Mean	Median	SD	Min	Max
Physicochemical habitat					
Surface area (ha)	146.4	33.1	311.7	4.1	2174.5
Watershed-to-lake area ratio	34.5	19.1	43.1	0.3	292.2
Mean depth (m)	3.0	2.8	1.5	0.8	11.5
Secchi depth (m)	1.2	1.1	0.8	0.2	6.1
Chlorophyll *a* (*u*g/L)	42.1	36.2	28.7	3.4	146.9
Total phosphorus (*u*g/L)	120.2	101.6	70.9	31.6	409.4
Total nitrogen (mg/L)	2.7	1.7	2.6	0.7	13.7
Total suspended solids (mg/L)	18.5	12.5	15.0	3.4	101.8
Rowcrop (%)	39.3	41.3	26.1	0.0	88.2
Catch-per-unit-effort					
Black crappie (number/NN)	7.3	2.5	12.7	0.0	91.2
Bluegill (number/NN)	7.8	4.1	12.0	0.0	80.5
Common carp (kg/NN)	1.6	0.0	3.8	0.0	27.1
Largemouth bass (number/hr)	79.7	65.0	69.8	0.0	393.3
White crappie (number/NN)	2.0	0.3	3.9	0.0	24.5
Proportional size distribution					
Black crappie	44	100	31.3	0	100
Bluegill	38	41	23.6	0	100
Common carp	74	87	32.1	0	100
Largemouth bass	53	50	23.7	0	100
White crappie	60	65	33.1	0	100
Relative growth index					
Black crappie	105	107	10.0	83	125
Bluegill	103	103	11.8	79	162
Common carp	103	102	16.4	77	133
Largemouth bass	95	95	7.0	71	113
White crappie	113	114	11.1	87	138
Relative weight					
Black crappie	99	98	8.1	72	117
Bluegill	100	99	8.0	85	123
Common carp	95	92	10.9	74	120
Largemouth bass	102	101	9.2	84	135
White crappie	96	97	8.5	81	113

Catch-per-unit-effort is presented as kilograms per fyke net night (kg/NN), number per fyke net night (number/NN), or number per hour of electrofishing (number/hour).

sampled. Catch rates for individual species varied from 0.0 to 393.3 fish/h, 0.0 to 91.2 fish/NN and 0.0 to 27.1 kg/NN (Table 1). Proportional size distribution varied from 0 to 100 and *Wr* varied from 72 to 135. Of the fish sampled in this study, 27,702 were aged and had mean RGI values from 71 to 162 among lakes. Mean *Wr* and RGI values were near 100, indicating good body condition and fast growth for most species.

Significant, nonrandom patterns in the abundance of common carp and sport fishes were observed and were particularly strong when considering bluegill and largemouth bass (Fig. 1). Although the threshold catch rate (i.e., *y*-axis value from the 2DKS) differed among the sport fish species, the threshold CPUE of common carp was consistently around 2 kg/NN. Several patterns in environmental characteristics for the different catch rate categories were observed across species (Table 2). With regard to watershed characteristics, the percentage of the watershed used for row-crop agriculture did not differ between high carp–low sport fish lakes and low carp–high sport fish lakes. Watershed to lake area ratios were also similar ($P > 0.07$) between catch rate categories for all species except bluegill, where lakes with high catch rates of common carp and low catch rates of bluegill had significantly lower ratios than low carp–high bluegill lakes. Differences in mean depth were similar for largemouth bass and bluegill categories where high carp–low bluegill or high carp–low largemouth bass lakes were significantly shallower than low carp–high bluegill or low carp–high largemouth bass lakes (Table 2). An opposite pattern was observed for black crappie and white crappie, though only the relationship for black crappie was statistically significant ($P \leq 0.05$). Secchi transparency was significantly lower and the concentration of total suspended solids was significantly higher ($P \leq 0.05$) in high carp–low sport fish lakes compared to low carp–high sport fish lakes for all species except white crappie. Chlorophyll *a* and cyanobacteria concentrations were significantly higher ($P \leq 0.05$) in lakes with high catch rates of common carp and low CPUE of bluegill, largemouth bass and white crappie. Similarly, total phosphorus and total nitrogen concentrations were highest ($P \leq 0.05$) in lakes with high catch rates of common carp and low catch rates of the other species. Lastly, RGI values for the study species were highest in lakes with high common carp catch rates and low catch rates of the study species (Table 2).

Nonmetric multidimensional scaling provided insight similar to that obtained using catch rate categories (Fig. 2). A 2-dimensional solution was found that had both low stress (7.64%) and low instability (<0.0001). The first axis was correlated with black crappie and largemouth bass catch rates, whereas the second axis was most closely related to CPUE of common carp and bluegills. Catch rates of white crappie were not highly correlated with either axis. High catch rates of largemouth bass, bluegill, black crappie and white crappie tended to occur in the same lakes and were typically lakes with low catch rates of common carp. The watershed to lake area ratio was the only variable significantly correlated ($P \leq 0.05$) with the first axis. Watershed to

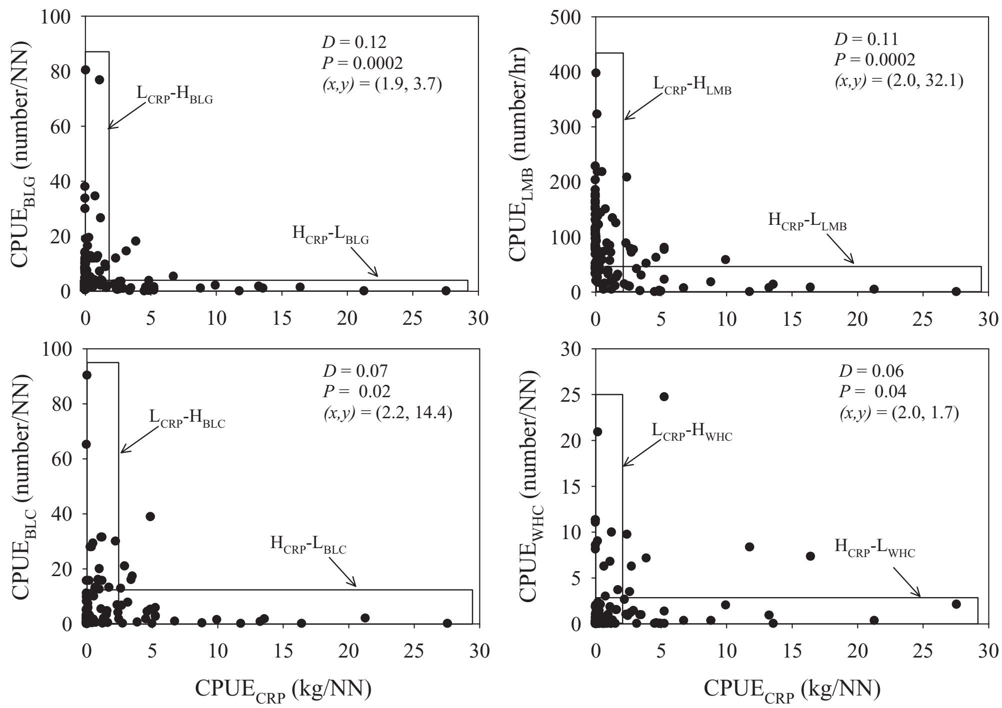

Figure 1.-Relationship between catch-per-unit-effort (CPUE) of common carp (CRP; kg per fyke net night [NN]) and CPUE of bluegill (BLG), largemouth bass (LMB), black crappie (BLC) and white crappie (WHC) sampled from 129 lakes across Iowa, 2001–2006. Boxes represent high (H) and low (L) catch rates defined by threshold catch rates (i.e., *x*, *y* value). Test statistics are the result from a 2-dimensional Kolmogorov-Smirnov test.

lake area ratio, mean depth, and Secchi depth were positively related to the second axis and concentrations of chlorophyll *a*, total phosphorus, and total suspended solids were negatively related to the second axis. Total nitrogen concentration and the percentage of row-crop agriculture in the watershed were not related to either axis. Common carp catch rates were highest in natural lakes and oxbows that had shallow depths, low watershed to lake area ratios, high total

Table 2.-Mean values for watershed to lake area ratio (WLA), percentage of row-crop agriculture in the watershed, depth (m), Secchi transparency (m) , total suspended solids (TSS; mg/L), chlorophyll *a* (chl *a*; μg/L), cyanobacteria (μg/L), total phosphorus (TP; μg/L), and total nitrogen (TN; mg/L) of 129 lakes sampled across Iowa, 2001–2006. Mean relative growth index (RGI) values are also provided.

	Bluegill		**Largemouth bass**		**Black crappie**		**White crappie**	
Variable	H_{CRP}-L_{BLG}	L_{CRP}-H_{BLG}	H_{CRP}-L_{LMB}	L_{CRP}-H_{LMB}	H_{CRP}-L_{BLC}	L_{CRP}-H_{BLC}	H_{CRP}-L_{WHC}	L_{CRP}-H_{WHC}
WLA	**16.6 (3.6)**	**41.5 (6.0)**	31.8 (6.0)	32.0 (4.9)	33.9 (8.3)	41.3 (8.7)	33.4 (7.1)	24.8 (9.2)
Row crop	45.1 (5.9)	38.4 (3.2)	39.6 (4.1)	43.5 (4.3)	47.9 (9.3)	40.8 (5.0)	45.2 (10.2)	36.3 (4.6)
Depth	**1.9 (0.2)**	**3.3 (0.2)**	**2.7 (0.3)**	**3.3 (0.2)**	**2.8 (0.3)**	**2.4 (0.2)**	2.8 (0.3)	2.5 (0.2)
Secchi	**0.7 (0.1)**	**1.4 (0.1)**	**1.0 (0.1)**	**1.5 (0.1)**	**0.5 (0.1)**	**1.1 (0.1)**	**0.6 (0.1)**	**1.1 (0.1)**
TSS	**30.3 (4.8)**	**13.9 (1.0)**	**24.5 (2.8)**	**11.2 (0.9)**	**28.4 (4.5)**	**23.5 (3.7)**	25.9 (4.9)	22.3 (3.2)
Chl *a*	**57.0 (7.9)**	**38.1 (2.8)**	**49.5 (4.7)**	**34.5 (3.2)**	58.8 (6.2)	51.8 (5.9)	**53.7 (6.0)**	**45.2 (5.2)**
Cyanobacteria	**238.2 (93.1)**	**109.0 (24.4)**	**216.1 (53.7)**	**66.8 (11.9)**	247.2 (103.0)	222.2 (74.0)	**313.9 (156.9)**	**97.4 (22.2)**
TP	**158.6 (17.1)**	**109.0 (7.6)**	**136.1 (11.4)**	**99.0 (8.9)**	**225.2 (26.5)**	**139.9 (13.9)**	133.1 (14.4)	125.2 (11.5)
TN	**2.9 (0.4)**	**2.5 (0.3)**	**3.1 (0.4)**	**2.2 (0.4)**	3.3 (0.5)	2.3 (0.2)	3.2 (0.4)	1.8 (1.7)
RGI	**110.5 (3.3)**	**100.0 (1.6)**	**97.1 (1.4)**	**94.0 (0.9)**	99.0 (3.2)	102.9 (3.3)	118.5 (2.8)	116.3 (4.0)

Values in bold are significantly different ($P \leq 0.05$) between lakes with high catch rates of common carp (H_{CRP}), low catch rates of bluegill (L_{BLG}), largemouth bass (L_{LMB}), black crappie (L_{BLC}) or white crappie (L_{WHC}) and lakes with low catch rates of common carp (L_{CRP}), high catch rates of bluegill (H_{BLG}), largemouth bass (H_{LMB}), black crappie (H_{BLC}) or white crappie (H_{WHC}). Number in parentheses represent one standard error.

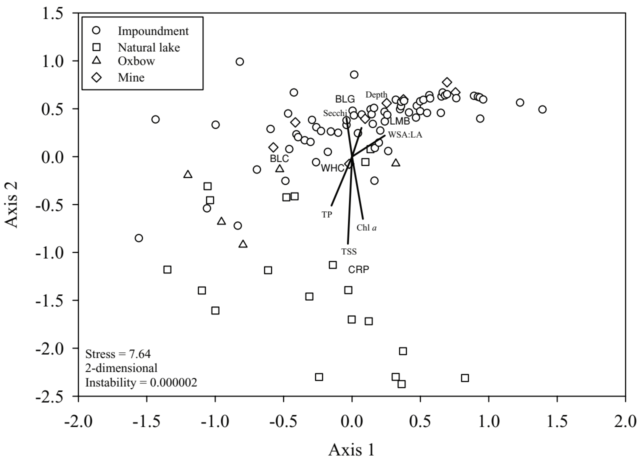

Figure 2.-Nonmetric multidimensional scaling (NMDS) ordination of 129 lakes sampled across Iowa, 2001–2006. The ordination is based on catch rates of common carp (CRP), bluegill (BLG), largemouth bass (LMB), black crappie (BLC) and white crappie (WHC). Variables significantly correlated ($P \leq 0.05$) with NMDS scores included Secchi disk depth (m), mean depth (m), watershed to lake area ratio (WSA:LA), chlorophyll *a* concentration (chl *a*; μg/L), total suspended solids (TSS; mg/L) and total phosphorus (TP; μg/L).

phosphorus and total suspended solid concentrations, and low water clarity. In contrast, bluegill and largemouth bass were typically most abundant in impoundments with low total phosphorus concentrations and high water clarity. Additional insight was gained by identifying individual lakes by the catch rate category for each species (Fig. 3). High carp–low bluegill or high carp–low largemouth bass lakes were almost exclusively natural lakes, while low carp–high bluegill or low carp–high largemouth bass lakes were primarily mines and impoundments. Although similar patterns were observed for black crappie and white crappie categories, more variation in lakes types with low catch rates of common carp and high catch rates of crappies was apparent.

Discussion

High densities of common carp were related to undesirable water quality conditions and low abundance of important sport fishes. Research on the ecological effects of common carp introductions has been conducted for nearly a century (Cahn 1929), and most research has shown significant deterioration of lake systems resulting from the direct and indirect effects of common carp (Schrage and Downing 2004). For instance, Lougheed et al. (1998) examined the effects of common carp in experimental enclosures placed in a marsh near the western edge of Lake Ontario and found that common carp increased turbidity, total phosphorus and total ammonia. Schrage and Downing (2004) reported efforts to remove benthivorous fishes (primarily common carp) from Ventura Marsh, a 76-ha marsh at the western end of Clear Lake, Iowa. Ventura Marsh rapidly switched from a turbid to a clear state following fish removal. Juvenile common carp became reestablished in the system within about 6 mo and the marsh reverted to a turbid state. These studies and others have thoroughly demonstrated how common carp increase phosphorus concentrations (Breukelaar *et al.* 1994), phytoplankton biomass and turbidity (Breukelaar *et al.* 1994, Lougheed et al. 1998), and reduce the occurrence and abundance of aquatic macrophytes (Hinjosa-Garro and Zambrano 2004). In turn, changes in physicochemical habitats result in fish assemblages dominated by species tolerant of poor water quality and reduce the abundance of sight-feeding predators (Zambrano et al. 2006). Our findings are consistent with this literature.

Enhanced water clarity is therefore an important management goal in agricultural regions. Although a number of methods and techniques are available to managers, manipulation of fish assemblages is one of the most common methods of enabling a system to change from a turbid to a clear state (Mehner et al. 2002). Our data suggest that common carp may be more abundant and therefore more of a management concern in natural lakes and oxbows (mostly shallow systems) than in impoundments and mines (deeper systems). From a management perspective, this is encouraging because nearly all research evaluating the success of biomanipulation efforts has found that management activities are more likely to be successful in shallow lakes than in deeper systems (Scheffer 1998). For example, Jeppesen et al. (1997) reviewed experimental, observational and simulation studies focused on Danish lakes. They concluded that manipulation of fish populations is most likely to have a more dramatic and long-lasting effect in shallow lakes than deep lakes. Similar results have been reported across North America and Europe (Mehner et al. 2002).

Compared to deep lakes, shallow lakes are more likely to experience (re)colonization of aquatic vegetation, which promotes clear water through several mechanisms. Phytoplankton, particularly cyanobacteria, is often present at low densities when high densities of macrophytes are present, possibly due to both direct and indirect suppression of phytoplankton populations by macrophytes (Jeppesen et al. 1998). Macrophytes provide refuge for zooplankton from fish predation, thereby reducing phytoplankton density via top-down mechanisms (Stansfield et al. 1997). Macrophytes may compete with phytoplankton for nutrients (Van Donk et al. 1990), reduce nitrogen availability for phytoplankton through denitrification in macrophyte beds (Van Donk et al. 1993) or excrete allelopathic substances against phytoplankton (Declerck et al. 2000). In addition to interacting

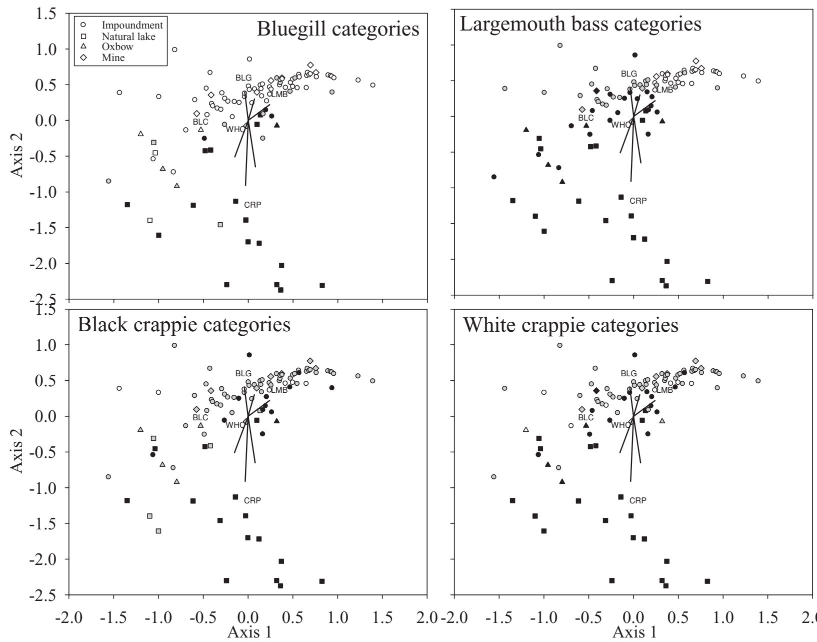

Figure 3.-Nonmetric multidimensional scaling (NMDS) ordination of 129 lakes sampled across Iowa, 2001–2006. The ordination is based on catch rates of common carp (CRP), bluegill (BLG), largemouth bass (LMB), black crappie (BLC) and white crappie (WHC). The ordination is the same as Fig. 2, except that symbols with different colors represent different catch rate categories for each species. White symbols represent lakes with low catch rates of common carp and high catch rates of sport fish (i.e., bluegill, largemouth bass, black crappie, white crappie). Gray symbols represent low catch rates of common carp and low catch rates of sport fish. Black symbols represent high catch rates of common carp and high catch rates of sport fish. Vectors represent water quality characteristics as provided in Fig. 2. ○ = impoundment; □ = natural lake; △ = oxbow; ◇ = mine.

with phytoplankton communities, macrophytes also help promote clear water conditions by reducing resuspension of sediment and other bottom materials with their roots and by buffering the effects of wind (Barko and James 1998).

Although the effects of common carp removal on lake systems has yet to be tested across a distribution of lake types in the midwestern United States, efforts focused on shallow systems are most likely to yield substantial, long-term changes in water quality characteristics and sport fish populations, particularly if measures are taken to reduce external nutrient delivery (Søndergaard et al. 2008). In addition to providing guidance on where restoration efforts should be targeted, this study suggests that benchmarks for common carp reduction must be considered within the context of ecological thresholds.

Ecological thresholds are points where an abrupt change in some property or process produces a large response in the ecosystem (Scheffer et al. 2001, Groffman et al. 2006). Because ecological thresholds are important in regulating population, community and ecosystem dynamics, understanding and identifying thresholds continues to be a major focus of theoretical and applied ecologists (Groffman et al. 2006). Experimental studies suggest that the effects of common carp on lake systems are not linear (Zambrano and Hinjosa 1999, Zambrano et al. 1999). Rather, the abundance of common carp seems to reach a threshold that once crossed causes abrupt changes in ecosystem characteristics. For example, Zambrano et al. (1999) evaluated the effects of common carp stocked into semi-natural ponds in Mexico and found that Secchi transparency, aerial coverage of aquatic macrophytes and density of epibenthic macroinvertebrates were inversely related to the relative abundance of common carp. A negative exponential model was used to describe each relationship; however, the patterns were nearly identical to those of common carp and sport fishes observed in the current study.

Although a nonlinear regression model could be fit to the relationship of common carp with sport fishes in Iowa lakes, we argue that the relationship is probably not continuous and functions as a threshold. Results of Zambrano and Hinojosa (1999) provide support for this contention where intermediate states of water clarity were not observed in response to common carp density in experimental ponds. Instead, ponds with different densities of common carp remained in either a turbid or clear state over the course of the experiment. When ponds did switch from a clear to a turbid state, the time to switch was extremely short. As such, the authors argued that the pond systems were regulated by a threshold density of common carp abundance. Regardless of the specific nature of the relationship (continuous or discontinuous), our study suggests that when common carp catch rates exceed 2 kg/NN, lakes in this region are likely to have high nutrients, poor water clarity and poor sport fish populations. While common carp are important with regard to water quality in Iowa lakes, control of common carp should be one component of an integrated water quality management program along with reductions in nutrient and sediment inputs from agriculture and other watershed disturbances.

Although much remains to be learned about the relations between fish, nutrients, water clarity and other characteristics (e.g., aquatic macrophytes) of agriculturally eutrophic lakes, this study provides insight into the management of lake systems in agriculture-dominated landscapes and the importance of ecological thresholds. In these eutrophic lakes, nutrient inputs and fish assemblage structure interact to influence nutrient dynamics, water clarity and ecosystem health.

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